

# ENDODONTOID LAND SNAILS FROM PACIFIC ISLANDS

(Mollusca: Pulmonata: Sigmurethra)

## Part II

Families Punctidae and Charopidae, Zoogeography

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# INTRODUCTION

This is the second of two monographs revising the endodontoid land snails of Polynesia, Micronesia, and Fiji. Part I, covering the older and larger family Endodontidae, reviewed 185 species-level taxa (Solem, 1976b). Subsequently (Solem, 1977a) I described *Protoendodonta laddi* and *Cookeconcha antiquus* from Late Pleistocene strata in core drillings on Midway Atoll and have three new subfossil *Pseudolibera* from Makatea (Solem, in preparation B). Together with the 98 species-level taxa belonging to the Families Punctidae and Charopidae diagnosed below, a total of 290 species-level taxa have been reviewed during this project. Describing the extensive Hawaiian Island monophyletic radiation of up to 290 unnamed, now mostly extinct, endodontid taxa preserved in the Bernice P. Bishop Museum is a task left to others.

The basic descriptive work essentially was completed in 1969, based on research supported by National Science Foundation grants G-16419, GB-3384, and GB-6779. This has been supplemented by modest materials received subsequently. As a by-product of the basic monographs, papers on a number of problematic groups (Solem, 1964a–b, 1968b, 1969b, 1972b, 1973c–d), extralimital endodontoids (Solem, 1958b, 1961, 1968c, 1970a, c, 1975, 1976a, 1977c, in preparation A), biogeography (Solem, 1958a, 1959a, 1968a, 1969c, 1973c, 1979a–b, 1981), endodontoid biology (Solem, 1969a, d, 1974), and fossil land snails have been prepared (Solem, 1977a, in preparation B; Solem & Yochelson, 1979).

In the early 1970s, the new availability of scanning electron microscopy (hereafter SEM) added a major new dimension to this project. A series of reports (Solem, 1970b, 1972a, c, 1973a–b, f, 1976a, 1977a–b) explored its potential, and extensive additional data has been incorporated into the major reviews. The first monograph was submitted for publication in December, 1973, and was issued in due course (Solem, 1976b).

Finishing Part II has involved making very difficult decisions as to where and when to terminate additional information seeking. The Endodontidae are restricted to the Pacific Islands and thus this monograph was easily circumscribed. Both the Punctidae and Charopidae have their main centers of diversity elsewhere, have been liberally supplied with generic and family-level names based on shell features and hunches, frequently have been rather poorly described and often never illustrated (particularly Iredale, 1913, 1933, 1937a–c, 1939, 1941a–c, 1942, 1944, 1945), and

essentially are unknown anatomically except for the data supplied by Hutton (1884a), Suter (see References), and Climo (1969a–b, 1970, 1971a–b, 1978) on New Zealand taxa and contributions on South African taxa summarized by Connolly (1939). I have dissected and partially illustrated more than 75 extralimital species in addition to those included below. This attempt to work out extralimital relationships and to assign subfamily and generic names is only a start toward producing an overall phylogeny and classification.

The limits finally adopted in Part II were: (1) to include all extralimital species known to belong in genera endemic to Polynesia, Micronesia, and Fiji; and (2) to include anatomical data on extralimital taxa only when needed to establish the subfamily units used in the systematic review and biogeography. Thus, 10 of the 98 taxa discussed here are found only in such areas as the New Hebrides, Solomon Islands, Bismarck Archipelago, West Irian, and Indonesia (six species of *Sinployea*, three species of *Lagivala*, and *Palline biakensis*), whereas another species, *Discocharopa aperta* (Möllendorff, 1888), occurs sporadically in the area covered (Fiji, Samoa, Austral and Society Islands) but has its main distribution from the Philippines to Australia. Data are presented on type genera or species of several nominate subfamilies from diverse areas (New Zealand, Juan Fernandez), but no attempt is made to provide an overall classification of the Charopidae in this monograph. There still are too many gaps in our knowledge of anatomy and shell structure.

By the early 1970s there still remained a few problem taxa. *Microcharopa* and *Discocharopa* showed many differences from the other Pacific Island taxa, but I had not been able to determine their affinities because only empty shells were available. In addition, there was the problem of *Stenopylis*, a second Philippine Islands to Australia taxon. Both *Stenopylis* and *Discocharopa* were known to occur in Central Australia. Planned fieldwork in Western and Central Australia in early 1974 hopefully would yield live material. Early dry season collecting near Alice Springs produced only dead shells, but museum records suggested that both genera had a wide distribution in North Australia. The probability of subsequently obtaining live materials seemed excellent. In addition, the possibility of field survey work in Micronesia for the Office of Endangered Species arose, which could have greatly expanded the anatomical coverage of the

Trukcharopinae and Semperdoninae. This prospect did not materialize, but in 1976 and 1977 additional field and dissection work in Australia permitted allocating *Discocharopa*, *Stenopylis*, and *Microcharopa* to family units. The writing of introductory sections and the biogeographic review, assigning table and plate numbers, and final editing were completed in 1978.

It is with a mixture of delight and regret that I conclude this systematic project—delight at the new information and ideas produced, regret that the hand of man has so altered the Pacific Island environment that future work on most of these taxa and testing of the new ideas presented has been rendered impossible by extinctions. The charopids apparently have been less affected than the Endodontidae, but even with these it is probable that many already are a vanished group of organisms.

Concluding this monograph is a detailed biogeographic review of the endodontoid land snails. This project spanned the time from the dominance of fixed continents as a biogeographic axiom to the current dogma of wandering continents. Land snails have not been versed in biogeographic controversies, and their patterns of distribution continue to fit neither model exclusively.

The endodontoid land snails were the most speciose land snail group on the Pacific Islands (Solem, 1976b, pp. 1–2). They still are the most speciose group in Australia and New Zealand (table XI), areas in which they seem to be flourishing despite human activities. The data and ideas presented in these volumes hopefully will inspire more investigations of these taxa.

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## PREVIOUS STUDIES

A more extensive historical review regarding the Pacific Island taxa was given in Solem (1976b, pp. 7–8) and should be consulted for background comments. Previously described charopid taxa date from the studies of Férussac (1840), Hombron & Jacquinot (1841), Mousson (1865, 1869, 1870, 1871), Cox (1870), Pease (1870), Garrett (1872, 1881, 1884, 1887a–c), Liardet (1876), Tapparone-Canefri (1883), Möllendorff (1888, 1900), Beddome (1889), Quadras & Möllendorff (1894), Smith (1897), Clapp (1923), Rensch (1937), Dell (1955), Ladd (1958, 1968), and Solem (1959a, 1960). Of the 45 previously described species-level taxa, 11 were named by Garrett, six by Möllendorff, five by Mousson, four by Quadras & Möllendorff, and four extralimital species by Rensch. The remaining 15 species are scattered among the other authors. The dates of species descriptions were summarized in Solem (1976b, p. 3, table III). The cluster of 1890 and 1900s taxa in the Charopidae reflects the activities of Möllendorff and his field associate, J. F. Quadras. The 10 taxa described since 1920 include the highly significant fossils from Eniwetok, *Vatusila eniwetokensis* (Ladd, 1958), and Funafuti, *Lagivala davidi* (Ladd, 1968), plus basically extralimital taxa (Solomon Islands, New Hebrides, Bismarck Archipelago) that happen to belong to genera also represented on the Pacific Islands. As with the Endodontidae, the greatest period of descriptive activity was in the 1870s and 1880s, reflecting the publications of Mousson and Garrett.

No data had been recorded in the literature concerning the anatomy of the Pacific Island taxa except for a few notes on the tail, jaw, and radula of *Russatus nigrescens* (Möllendorff, 1900, p. 108, figs. 1–3) and the radula and penis complex exterior of *Sinployea euryomphala* (Solem, 1959a, pl. 6, figs. 7–8).

Because the main center of the charopid radiation is extralimital to the Pacific Islands, extensive reference has had to be made to taxa from other parts of the world. New Zealand, Australian, and New Caledonian

taxa in particular have yielded important comparative data. Rather than detail the many reports here, citations are given under the organs or species referred to at that place in the text. Here it is necessary only to point out that these are diverse faunas with a long record of study. The literature is highly fragmentary and widely scattered, but fortunately there are summary references that enable relatively quick access to the literature. For New Zealand, the classic monograph of Suter (1913) and the checklist of Powell (1976) summarize the work done prior to the highly significant studies of Climo (1969a–b, 1970, 1971a–b, 1978). For Australia, the checklist of Iredale (1937a–c) and his faunistic reviews of nearby areas as well as Australia (Iredale, 1939, 1941a–c, 1942, 1944, 1945) provide essential but very difficult to use reports. Franc (1957) and Solem (1961) supplement the excellent review of New Caledonian land mollusks given by Crosse (1894).

Early observations on the anatomy and radular structure of some Australian (Hedley, 1891, 1893) and New Zealand (Hutton, 1884a, Suter, 1890, 1891a–b, 1892a–c, 1893a–d, 1894a–d, 1901, 1903, 1913) charopids were accurate within the limits of optical observation and the state of knowledge concerning molluscan anatomy extant at that time, but have little value today in deciding generic and family limits.

Even more than for the Endodontidae, the classification of the charopids used previously was based on form “pigeon holes,” and the assignments made to genera were based upon superficial conchological similarities. Of the 21 genera reviewed below, only two were named previously, and both of them, *Punctum* Morse, 1864, and *Discocharopa* Iredale, 1913, are genera whose main distributions lie outside the Pacific Island area. All the remaining species belong to undescribed, endemic taxa, mostly not yet known from other than the fringing islands and Pacific Island area proper.

## MATERIAL STUDIED

The 98 taxa formally described or alluded to as probably representing new taxa were represented by about 7,500 specimens. Since the summary presented by Solem (1976b, p. 9), a number of charopids from the Lau Archipelago of Fiji collected by Price in 1970 and Cernohorsky in 1977, Society Islands by Solem in 1977, Western Australia by Solem, L. Price, and Carl Christensen in 1976 and 1977, and near Alice Springs in the Northern Territory in 1974 and 1977 have become available. Data from them has been incorporated into the systematic review. No attempt at recalculating the data in Solem (1976b, pp. 9–10, tables IV–V) has been made because the numbers added are small in comparison to the previously listed materials.

Throughout the text, the following abbreviations are used to indicate the repository of the cited specimens:

AIM	Auckland Institute and Museum, Auckland
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
BPBM	Bernice P. Bishop Museum, Honolulu
DMW	National Museum of Natural History, Wellington
FMNH	Field Museum of Natural History, Chicago
IRB	Institut Royal des Sciences Naturelles de Belgique, Brussels
JDCP	Collection of <i>Journal de Conchyliologie</i> , Paris
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MSNG	Museo Civico di Storia Naturale "Giacomo Doria," Genova
NHM	Naturhistorisches Museum, Basel
NMWC	National Museum of Wales, Cardiff
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
RSM	Royal Scottish Museum, Edinburgh
SAM	South Australian Museum, Adelaide
SMF	Natur-Museum Senckenberg, Frankfurt-a.-M.
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

WAM	Western Australian Museum, Perth
ZMA	Zoologisch Museum, Amsterdam
ZMB	Zoologisches Museum der Humboldt-Universität, Berlin
Zurich	Zoologisches Institut der Universität, Zurich

Most of the material in the BPBM resulted from the historical activities of Andrew Garrett plus specimens obtained during three major expeditions in the 1930s. The Mangarevan Expedition from April 15 through October 28, 1934 (Cooke, 1935), Micronesian Expedition from December 8, 1935, to June 10, 1936 (Gregory, 1936, p. 40), and the Henry G. Lapham Expedition to Fiji from June 27 through September 28, 1938 (Buck, 1939, pp. 29–30), contributed major materials for this study. Additional collections made in Fiji by Harry G. Ladd, plus miscellaneous samples taken by a variety of BPBM staff members, combined with the above to provide the bulk of material analyzed.

Fieldwork sponsored by FMNH and National Science Foundation in Rarotonga (1964 and 1965), Western Samoa (1965), Fiji (1965 and 1970), Tonga (1965–1966), New Caledonia (1967), and New Hebrides (1972) by Laurie Price and/or Alan Solem was designed to sample areas that were underrepresented in the BPBM collections. Fieldwork in New Zealand (1962, 1965) and various parts of Australia (1962, 1965, 1973, 1974, 1976–77) provided critical comparative materials that enabled assigning subfamily names and indicating possible phylogenetic trends within the Arionacea. Only a few of these dissections are illustrated or cited here because this report is deliberately restricted to the Pacific Islands, except where a genus extends extraliminally.

Special features regarding the methods of collecting and specimen storage used by the BPBM staff were reviewed by Solem (1976b, p. 10) and are not repeated here, although applying in full to the studied materials used in this report.

## METHODS OF ANALYSIS

The basic data on distribution of size and shape variation within a population, how to recognize an adult shell, the limits of measurement reliability, and definitions of the standard measurements used were fully explained in Solem (1976b, pp. 11–15).

It is necessary to emphasize some data concerning sample bias because rather significant mean size differences among museum lots of previously described species are sometimes ignored. Prime examples of this are in such Rarotongan taxa as *Sinployea proxima* (Garrett, 1872) (table XX), *S. rudis* (Garrett, 1872) (table XXIII), *S. harveyensis* (Garrett, 1872) (table XXII), and the Funafuti Atoll *S. ellicensis ellicensis* (table XXIX). The pattern of trading samples from larger series to other museums or collectors still is common practice among conchologists. Larger specimens will tend to be retained by the original source, with smaller examples being dispersed widely. The possible extent of such dispersal is perhaps best illustrated by the endodontid land snail species *Libera tumuloides* (Garrett, 1872). Although "over 300 specimens" were collected originally, only 72 could be located for this study, indicating dispersion and loss or at least absence from major museum collections of more than 228 examples in less than 100 years (Solem, 1976b, p. 430). In contrast, the endodontid *Mautodontha* (M.) *zebrina* (Garrett, 1874) was known from "a half dozen specimens," all of which were located (Solem, 1976b, p. 162). Hence the reliability of mean measurements made on rare species is apt to be much greater than the means for common species where trading bias probably has distorted the data base. The exact extent of this distortion is unknown because the original measurements were generally of only a single specimen and were cited to the nearest millimeter. It must be recognized that sizes cited here for pre-1900 species may be larger than the means of the populations from which they came, but how much larger is unknown.

Data from the BPBM and FMNH collections involved measuring field samples that had not been diluted by trading activities. Thus, these results are directly comparable with each other.

For each adult specimen, shell height, diameter, whorl count, umbilical width, number of radial ribs on the body whorl, number of apical spiral cords, and any information concerning number and position of apertural barriers were recorded. The only difference in data recording from that used in Solem (1976b) is the consistent counting of body whorl ribs and apical cords.

The lack of apertural barriers in many charopids suggested greater use of sculptural features, and thus body whorl ribs were counted wherever possible. Solem (1976b, p. 14, fig. 5; p. 43, fig. 32; p. 52, fig. 36) defined each of these parameters except for the apical spiral cord count because the Endodontidae normally lacks this type of major sculpture. This count was taken on a suture-to-suture transect just before the end of the apex, provided that portion of the shell was unworn. At the start of the apex the exposed portion of the whorl profile is narrower than at the end, producing a significantly lower spiral ridge count. In *Microcharopa mimula* (fig. 4a), for example, the apex tip shows 15 ribs, and the apex end, 20 ribs. Usually, if a count could not be made near or at the usual position, the apex was sufficiently worn so that no count could be obtained. Apical cord count could not be tallied on many specimens. It was, in general, subject only to minor error in tallying where countable.

Height/Diameter (hereafter H/D) ratios, Diameter/Umbilical Width (hereafter D/U) ratios, and Ribs/mm. of body whorl circumference were calculated, the latter by the formula:

$$\text{Ribs/mm.} = \frac{\text{rib count on body whorl}}{\pi \times \text{shell diameter in mm.}}$$

The validity of this index was discussed by Solem (1976b, pp. 42–43).

Means, ranges, and standard errors of the means were computed for each parameter except whorl count for each population. Some of these results are presented in tables headed "Local Variation in . . . ." The total variation within each species or subspecies is summarized in tables headed "Range of Variation in . . . ." Means are given, but no standard errors of the mean were calculated because of the wide temporal span (1820 to 1977) of the materials represented.

At a later stage in this review, from eight to 12 examples of each species, where sufficient materials were available, were measured as to spire elevation and body whorl width, with a suitable ratio (SP/BWW) calculated and included in the "Range of Variation. . . ." tables. This gives an index of actual spire elevation undistorted by differences in the degree of body whorl descension behind the lip (see Solem, 1976b, pp. 24–26). At the same time these additional measurements were made, the pattern of the microsculpture on the early portion of the body whorl (see Solem, 1976b, p. 42, fig. 32b) and the pattern of rib spacing were determined and added to the draft diagnoses and descriptions.



Dissections of as many taxa as possible were carried out between 1961 and 1977, with several rechecks of structure as my understanding of the variation patterns increased. Because only fragmentary preserved animals were available for many species (see Solem, 1976b, p. 19), often only data on the terminal portions of the genitalia could be presented. Where possible, usually both the entire genitalia and the penis complex interior plus the pallial region were illustrated. Data on body color, tail structure, muscle system, and radular structures were obtained, but have not been illustrated because of lesser information content for classification and phylogeny. Unfortunately, the bulk of the dissection, illustration, and descriptive work was done prior to the availability of scanning electron microscopy as a research tool. Hence only a modest number of SEM observations are included in this study, although extensive use has been made of the SEM in working with materials from extralimital areas.

The data base consists of many shell observations and measurements, data from the pallial region, genitalia, radula, and external body features. In the previous report, some use was made of computer-generated phylogenies (Solem, 1976b, pp. 114–117, figs. 59–61). No such attempts were made in studying the Charopidae, because major features such as the apertural barriers obviously arose independently in several lineages (Solem, 1973b, p. 305), there were sharp anatomical differences between major groups with highly similar shell features, and the resulting convergences would utterly confuse any phenetic program unless *de post facto* elimination of convergences was undertaken. The benefits of the computer modeling outlined by Solem (1976b, pp. 114–117) were applied to this analysis without the work of programming and running various combinations. Mean measurement data was key-punched and numerous print-outs prepared, but this was essentially an aid to the phylogenetic analyses. Cladistic analysis was not attempted, because there are still numerous gaps in knowledge of the extralimital taxa. Outgroup comparisons would have been sketchy or incomplete at best, since the large charopid and punctid faunas of New Zealand, Australia, New Caledonia, and associated islands occur under conditions of complex sympatry, with many interspecific adjustments in penial chamber features that make interpreting relationships exceedingly difficult.

The result is that the proposed phylogeny has been arrived at by phylogenetic methodology after looking at a large number of characters in several organ systems and interpreting these according to the basic three-tiered pattern of evolutionary events outlined in Solem (1978b). I have used a pragmatic rather than an ideologic approach.

The problem of how to determine species limits when allopatric island populations are involved is quite difficult (Solem, 1976b, pp. 15–17). Sympatric congeneric species pairs or trios are invaluable in pre-

dicting the probability that two allopatric populations are or are not reproductively compatible. Since the Charopidae, as do the Endodontidae, use the surface features of the penis chamber and lower female tract for species recognition when two closely related species are sympatric, there usually are demonstrable differences in this region of the reproductive tract. Correlated with this will be minor to prominent shifts in conchological structures. By determining the "minimum conchological difference" between sympatric congeneric species pairs, a pragmatic standard is available against which to measure the degree of conchological difference between allopatric populations. If they equal or exceed the "minimum conchological difference," they are presumed to have diverged genetically to the level of species. If they show slight differences that are below the "minimum conchological difference," they are judged to be conspecific or at most subspecifically separable. Under conditions of allopatry there are few to no selective pressures for changes in the species recognition features of the genitalia. Indeed, there probably is rather strong selective pressure for maintaining a conservative pattern of species recognition features because departure from the pattern might be a mating disadvantage.

This methodology does not presume genetic linkage between conchological differences and species recognition features. Quite the contrary pattern is hypothesized. The conchological differences are linked to physiological or behavioral traits that have been selected for by environmental pressures, producing eventual basic genetic incompatibility. Upon becoming microsympatric with a congener, strong selective pressure for species recognition changes would exist, if, as seems probable, nonmultiple mating is a standard pattern for the charopids. Although we have no data on the frequency of mating, the absence of any evidence of more than one set of transferred sperm during dissection of several hundred individuals suggests that limited mating, rather than multiple mating, is more probable.

There are far fewer clear examples of congeneric sympatry with adequate materials for dissection in the Charopidae than in the Endodontidae (see Solem, 1976b, pp. 80–83, tables LII–LIV). Partly this reflects the difference in the distribution and probable age within the area. Partly this reflects a greater vertical range in habitat for the Charopidae, with tree trunk to semiarboreal habitat available even at dryer elevations for the charopids as contrasted with the terrestrially limited endodontids. Partly it is a matter of the Charopidae, except for *Sinployea*, showing rather low speciation but high generic diversity within the Pacific Island area. The one island on which an apparent multitude of species in one genus existed, Rarotonga, apparently has nine of 11 charopid species extinct.

The example that comes closest to being sympatric and showing minimal conchological differences involves *Sinployea peasei* and *S. avanaensis* on Raro-

tonga. The shell of *S. avanaensis* (fig. 45d–f) has more than twice the number of radial ribs on the body whorl, a distinctly narrower umbilicus, and averages about one-quarter whorl less, although it is nearly identical in size and shape. Anatomically, the penis of *S. avanaensis* is 1.4–1.6 mm. long, compared with 1.1–1.3 mm. in *S. peasei*; the verge (PV, fig. 43e) and muscle collar of *S. avanaensis* are larger than the equivalent structures in *S. peasei* (fig. 42d–e); and the pallial region of *S. avanaensis* (fig. 43b) is slightly shorter, with a noticeably shorter and broader rectal kidney arm than in *S. peasei* (fig. 42c). The two species apparently have ecological separation, with *S. peasei* found almost without exception under rotting wood and stones, whereas, except at a very dry station, *S. avanaensis* lived in moss and lichens on tree trunks. More detailed collecting in Avana Valley on Rarotonga is needed to determine if they are actually sympatric at any point or if they are microallopatric in their distribution.

In the Lau Archipelago of Fiji, for example, both *S. inermis* (Mousson, 1870) and *S. adposita* (Mousson, 1870) have been collected on Lakemba, Aiwa, and Yangasa Levu, and fragmentary material adequate for dissection of both species from a single island was available. The penis length of *S. inermis* is 0.8–1.0 mm. compared with 1.65 mm. for *S. adposita*, and the shells are very distinctive. The differences are larger than in the Rarotongan example. *Sinployea adposita* has a normal vergic papilla and a very small stimula-

tory pad, whereas *S. inermis* has a large stimulatory pad and a small vergic papilla.

On Mt. Lamalan, Guam (Station 137), both *Himerconcha lamalanensis* and *H. fusca* (Quadras & Möllendorff, 1894) were taken alive. The former has a shortened penis (2.0 mm.) with major pilasters forming halfway from epiphallic pore to atrium, and the latter has a longer (2.7 mm.) penis with the major pilasters starting just below the epiphallic pore (compare fig. 103a–b, d, f). These differences would serve quite effectively as species recognition devices.

Fortunately, differences between species in the Pacific Island Charopidae appear to be rather striking and uniform, although often difficult to characterize verbally because of extensive local variation.

Basically the same procedures and philosophical approach were used to study both the Charopidae and Endodontidae, so that the results are directly comparable in terms of species discrimination, classification, and phylogenetic interpretations. The greater generic diversity and usually lower specific diversity in the Pacific Island Charopidae are interpreted as resulting from multiple invasions from other areas at a more recent time than for the Endodontidae, plus the probable fact that the Helicarionidae and Euconulidae may have been invading only slightly later in time than the Charopidae. Conceivably, this often arboreal group of Limacacea could have denied the opportunity for extensive arboreal radiation to the Charopidae.



# PATTERNS OF MORPHOLOGICAL VARIATION

Initial studies from 1961 through 1969 on both shell and anatomy were carried out at 100× magnification or less using a Leitz dissecting microscope. Radular mounts in Euparal were examined unstained using a Leitz Ortholux compound microscope under bright-field, dark-field, and phase-contrast illuminations. Subsequently, SEM observations on both shell and radular features resulted in a series of reports (Solem, 1970b, 1972a–c, 1973a–b, d, 1974, 1975, 1976a, 1977a–b) whose results are partially incorporated here.

None of the available anatomical material was suitable for histological investigation. In many cases the apical genitalia of the BPBM material could not be studied because of the preservation technique utilized (Solem, 1976b, p. 19).

The following survey of shell and anatomical variation is less detailed than that presented for the Endodontidae (Solem, 1976b, pp. 19–99). Instead of one phylogenetic lineage being represented, the Pacific Island Charopidae include several independent lineages. Instead of a monophyletic origin for the apertural barriers, several independent origins are involved. Thus, certain of the questions asked in the endodontid review are not relevant and were omitted. In terms of shell structure, the Charopidae on the Pacific Islands simply are more conservative.

## SIZE AND SHAPE VARIATIONS

At least one specimen was seen of all the species treated in this monograph, so that the discussion that follows includes all the named taxa. Specimens that were indicated as probably representing new taxa, but which were not formally named, have been omitted from the comments and statistical analyses. No attempt at use of factor or multivariate analysis has been attempted because only the relatively crude standard shell measurements were available. The overall pattern of mean measurements of each species follows that of the Endodontidae (Solem, 1976b, pp. 20–21, figs. 6–10) except that they are more centrally clustered. Table I summarizes the basic distribution for nine variables or ratios. Although the extremes are well removed from the median, the distance between the first and third quartiles is relatively restricted. For shell height, diameter, and H/D ratio the first to third quartile range is 18%–19% of the total range, for the whorl count it is only 13%, for apical cords only 16%, and for the number of ribs on the body whorl (assuming the maximum as 200) and body width it is 22.5%. Consid-

TABLE I. – RANGE OF VARIATION IN THE PACIFIC ISLAND CHAROPIDAE.

	Minimum	1st Quartile	Median	3rd Quartile	Maximum
Means of:					
Height	0.48	1.23	1.51	1.81	3.69
Diameter	1.07	2.27	2.76	3.49	7.52
H/D Ratio	0.365	0.486	0.523	0.566	0.801
Whorls	3 1/8+	3 7/8	4 1/8–	4 3/8–	6 5/8
D/U Ratio	2.03	3.44	3.94	4.73	CLOSED
Ribs on body whorl	18.9	74.0	91.1	115.0	REDUCED
Ribs/mm.	1.70	7.66	11.25	14.61	REDUCED
Body Whorl Width	0.32	0.76	0.90	1.15	2.06
Apical Cords	6.5	9.5	10.5	12.0	22.0

ering that four phyletic lines are clumped, this is a quite narrow basic range of variation. It is also much less than in the Endodontidae (Solem, unpublished data). The extent to which this results from distortions of the brood chamber formation as opposed to the much larger number of taxa and greater age of the Endodontidae is unknown.

Body whorl contour in the Charopidae shows the same type of variation found in the Endodontidae but differs in frequencies. Table II contrasts the two families, using the same definitions as for the character states in the Endodontidae except for omitting the brood chamber condition that has no Charopidae equivalent. Lateral compression, angulation, or carination of the periphery is far more prevalent in the

TABLE II. – BODY WHORL CONTOUR IN ENDODONTIDAE AND CHAROPIDAE.

Body Whorl Contour	Total Number of Taxa:	
	Endodontidae	Charopidae <sup>1</sup>
Laterally compressed	38	6
Evenly rounded	43	41
Flattened above and/or below rounded periphery	21	39
Angled periphery	14	1
Carinated periphery	28	3

<sup>1</sup>State not recorded for several taxa.

Endodontidae. The Charopidae almost all have either an evenly rounded periphery or a mild to prominent, *Sinployea canalis* (Garrett, 1872) (fig. 49b), lateral flattening above a rounded periphery. A very few species, such as *Sinployea planospira* (Garrett, 1881) (fig. 46e), have a clearly laterally compressed periphery. Only *Sinployea angularis* (fig. 64e) has an angled periphery, whereas *Himeroconcha quadras* (Möllendorff, 1894) (fig. 105b), *H. fusca* (Quadrass & Möllendorff, 1894) (fig. 105e), and especially *Maafu thaumasius* (fig. 76b) have carinated peripheries. These differences in peripheral contour obviously are not exclusive and have no value in trying to characterize the families, except to point out another area in which their average pattern of growth diverges. In the Endodontidae there was a noticeable effect on shell diameter and H/D ratio with changes in body whorl contour (Solem, 1976b, p. 23, fig. 14). The same pattern applies to the few Charopidae with drastically altered contours, but the numbers are too few to warrant statistical treatment.

Because there are significant differences between the families in terms of spire protrusion, a comparison is given on pp. 38–40. The only really high-spined charopid is *Ba humbugi* (fig. 74b). The only truly sunken spire in the Charopidae is found in *Roimontis tolotomensis* (fig. 91a), three additional species have the spire depressed below the body whorl (*Maafu thaumasius*, fig. 76a–b; *Himeroconcha lamlanensis*, fig. 104d–e; *Kubaryiellus kubaryi*, fig. 89a–b), and 11 taxa have the spire barely emergent to slightly depressed or actually variable in the case of *Lagivala demani* (Tapparone-Canefri, 1883). The differences in spire elevation are so minor that no analyses of possible effects on basic measurements are presented.

Umbilical shape in the Charopidae is monotonously V-shaped, becoming saucer-shaped when more widely open as in *Discocharopa* (fig. 36c) and nearly U-shaped in the few species where it is narrowed (figs. 41c, 51f). There is none of the rich variation seen in the Endodontidae (Solem, 1976b, p. 27, fig. 16), hence only a few comments were presented in the family comparisons (p. 40).

Many of the Charopidae tend to develop a columellar and basal callus upon cessation of growth. This has the effect of covering over threadlike apertural barriers on the columellar wall and basal lip. Much of the variation in presence or absence of a threadlike columellar barrier recorded in Table V probably is directly caused by the degree of basal callus formation. It shows particularly clearly in the illustrations of *Paline biakensis* (fig. 96b), *P. micramyla* (fig. 95d), *P. notera palauana* (fig. 94e), and *Vatusila kondoi* (fig. 82b). In complete contrast, taxa such as *Kubaryiellus kubaryi* (Möllendorff, 1900) and *Russatus nigrescens* (Möllendorff, 1900) (fig. 89b, e) totally lack any trace of such a callus.

A final comment is required concerning the development of sulci on the whorls and the very unusual canalization of the sutural area. In the Endodontidae

(Solem, 1976b, pp. 51–52) development of a subsutural and/or subperipheral sulcus is primarily associated with keel formation. In the two sharply keeled Charopidae, *Maafu thaumasius* (fig. 76a–c) and *Himeroconcha quadras* (Möllendorff, 1894) (fig. 105b), quite prominent sulci are present both above and below the periphery. In *H. fusca* (Quadrass & Möllendorff, 1894) (fig. 105e), which is much less sharply keeled, only a weak suprapерipheral sulcus is present. In the one species with angulated periphery, *Sinployea angularis* (fig. 64e), there is a clearly defined subsutural sulcus, and in both *Vatusila kondoi* (fig. 82b) and *Sinployea rudis* (fig. 47e), which have rounded peripheries, there are distinct suprapерipheral sulci. They are the only equivalent to the unusual sulcus formation reported in the endodontid genus *Ancyodontia* (Solem, 1976b, p. 51, figs. 81d–e, 83, 86a, c, 88a, c, 89a). The functional significance, if any, of this last development is unknown.

A most unusual modification involves canalization of the suture. This is more clearly seen in *Sinployea proxima* (Garrett, 1872) (fig. 46a–b) where it is accomplished by slight detachment of at least part of the body whorl and creation of a narrow channel at the suture. This also occurs in *Lagivala macroglyphis* (Rensch, 1937) (fig. 81d–e), where the channel is formed by detachment to a greater angle and thus is shallower and wider, and to a barely detectable extent in *L. microglyphis* (Rensch, 1937). The same phenomenon is seen in the New Caledonian species *Andrefrancia alveolus* (Gassies, 1881) (Solem, 1961, pp. 454–456, fig. 12) and to a lesser extent in some Australian and New Zealand taxa. There is no equivalent change in the Endodontidae.

#### SHELL SCULPTURE

Data on the basic method of sculpture formation, apical sculpture type, and sculpture spacing is presented on pp. 40–41 as part of the family comparison discussion. In general the postapical sculpture in the Charopidae is relatively uniform in composition. It consists of major ribs, a few microradials in between, and fine microspirals segments that act as lateral supports to the microradials (figs. 1d–e, 2b, d), much in the same way as the buttresses to the microradials found in *Ptychodon microundulata* (Suter, 1890) (Solem, 1970b, pl. 59, figs. 9–11). The latter are quite different from the microspirals found in the Endodontidae, but this difference can be investigated only with the SEM. In some of the charopid species with reduced radial sculpture, such as *Himeroconcha*, these microspirals become enlarged into essentially continuous spiral cords. Again, this is far less specialized than in some of the situations found in the Endodontidae.

As an example of the specializations in microspiral elements, compare Figures 1d–e, 2d, and 3b, e. In *Sinployea modicella* (Férussac, 1840) (fig. 1d–e) the microspirals are on both sides of the radial riblets and tend to be joined medially and form minor cordlets. In



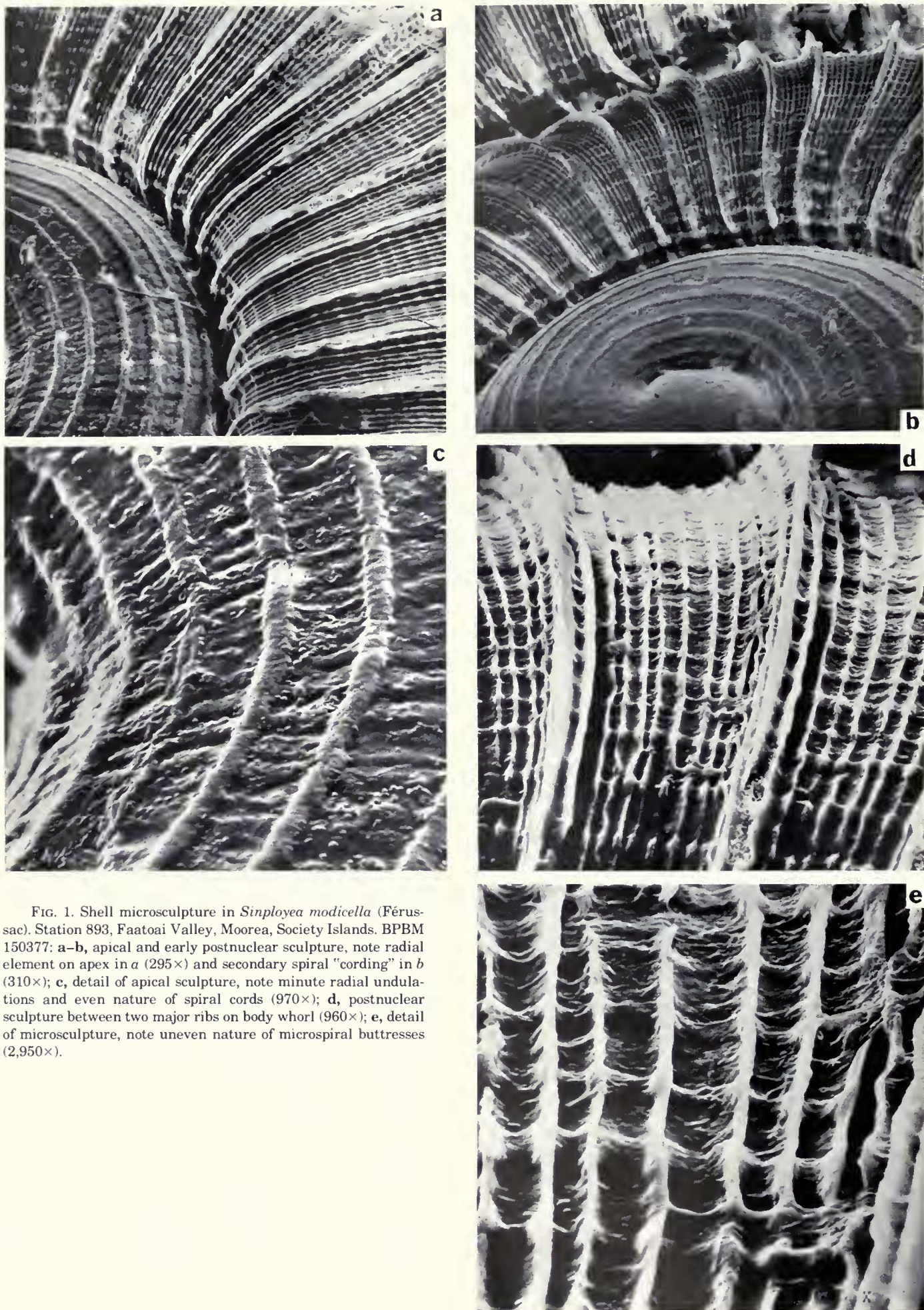


FIG. 1. Shell microsculpture in *Sinployea modicella* (Férussac). Station 893, Faatoai Valley, Moorea, Society Islands. BPBM 150377: a–b, apical and early postnuclear sculpture, note radial element on apex in a (295 $\times$ ) and secondary spiral "cording" in b (310 $\times$ ); c, detail of apical sculpture, note minute radial undulations and even nature of spiral cords (970 $\times$ ); d, postnuclear sculpture between two major ribs on body whorl (960 $\times$ ); e, detail of microsculpture, note uneven nature of microspiral buttresses (2,950 $\times$ ).



contrast, *Tuimalila pilsbryi* (fig. 2d) shows some of the same kind, but in the same inter-rib area it can have the microspirals as buttresses on only one side of the microradial. *Palline biakensis* (fig. 3b, e) and *Microcharopa mimula* (fig. 4a) have very minor actual surface microspiral elements (fig. 3e), simply a very narrow support ridge leading up to the top of the microradial whose upper edge then expands into an elon-

gated bead (fig. 3e) upward along the riblet. These "beads" appear, when viewed at lower magnification (fig. 3b), to form microspiral "cords" that at optical magnification are equivalent in aspect to the serrated edges on the microriblets in the endodontid *Australdonta raivavaeana* Solem (1976b, p. 33, fig. 23a-d). In both situations the spiral sculpture is barely visible at 100 $\times$  magnification, and determination of the compo-

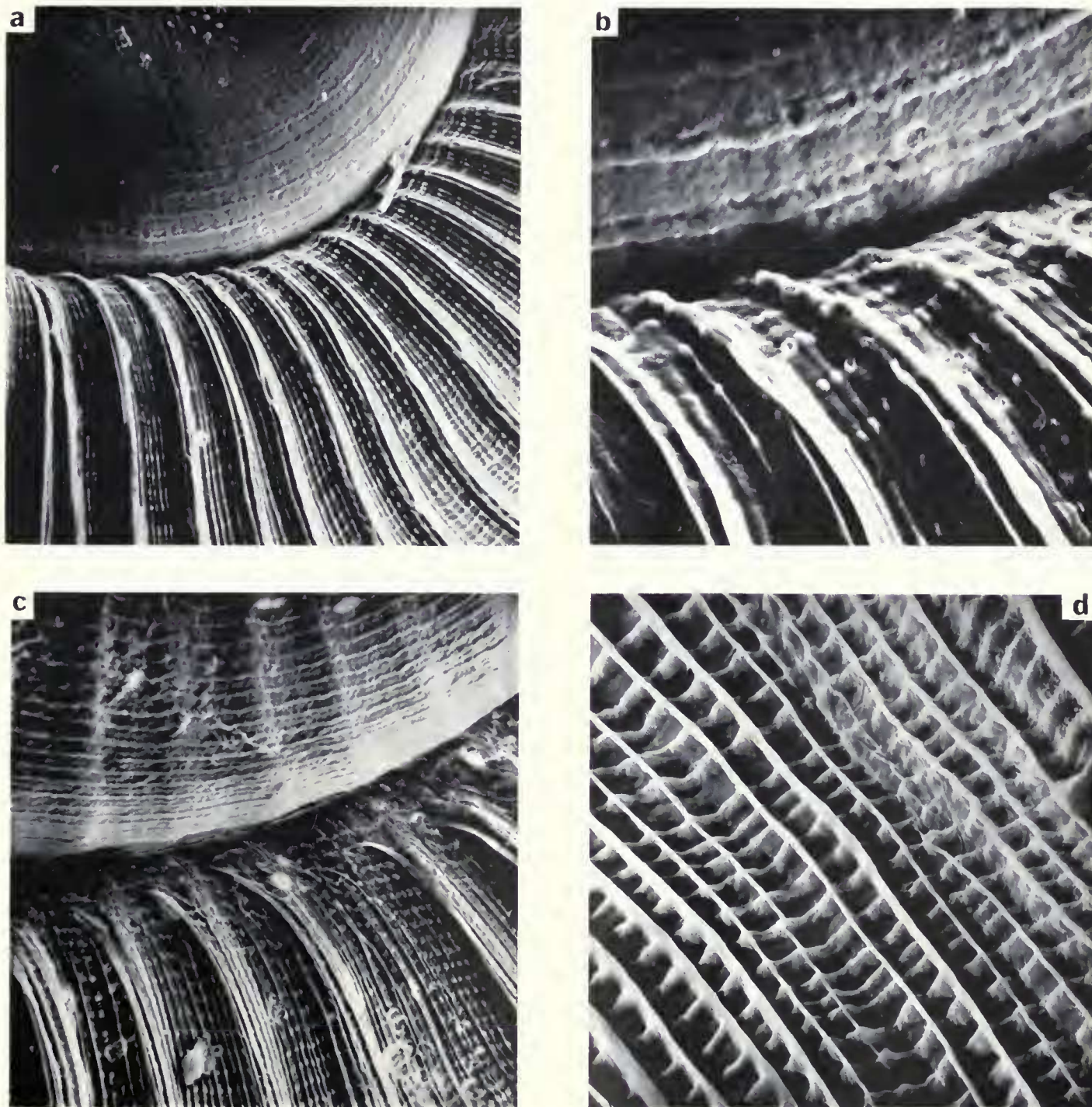


FIG. 2. Shell microsculpture in *Sinployea peasei* and *Tuimalila pilsbryi*: a-b, *Sinployea peasei*. Station 14, Avana Valley, Rarotonga, Cook Islands. FMNH 144613. a, apex and early postnuclear sculpture (320 $\times$ ); b, suture between apex and first postnuclear whorl, note beaded secondary spiral "cording" and waved effect of apical cords caused by conforming to minute radial undulations on surface (1,065 $\times$ ); c-d, *Tuimalila pilsbryi*. Station T-22, east side of Eua, Tonga. FMNH 152378. c, Apical and early postnuclear sculpture, note definite, widely spaced large radial swellings on apex, reduced size of spiral cords (320 $\times$ ); d, postnuclear sculpture on body whorl, note varying height of microspiral buttresses (1,065 $\times$ ).





**a**



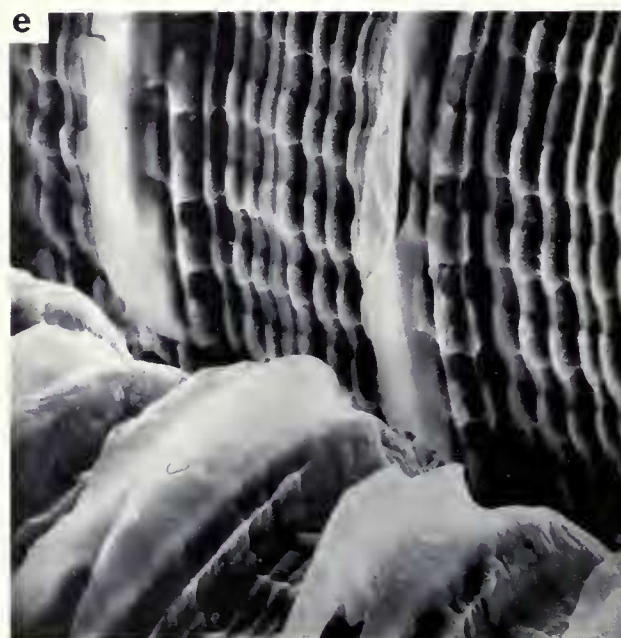
**b**



**c**



**d**



**e**

FIG. 3. Shell microsculpture in *Palline biakensis*. Hospitaal-grot, Biak, West Irian. Holotype. Rijksmuseum van Natuurlijke Historie, Leiden: **a**, apical and early postnuclear sculpture (275  $\times$ ); **b**, 1st and 2nd postnuclear whorls (280 $\times$ ); **c**, detail of apical-1st postnuclear whorl suture (930 $\times$ ); **d**, end of apical shell sculpture (920 $\times$ ); **e**, detail of sutural area between 1st and 2nd postnuclear whorls (910 $\times$ ).



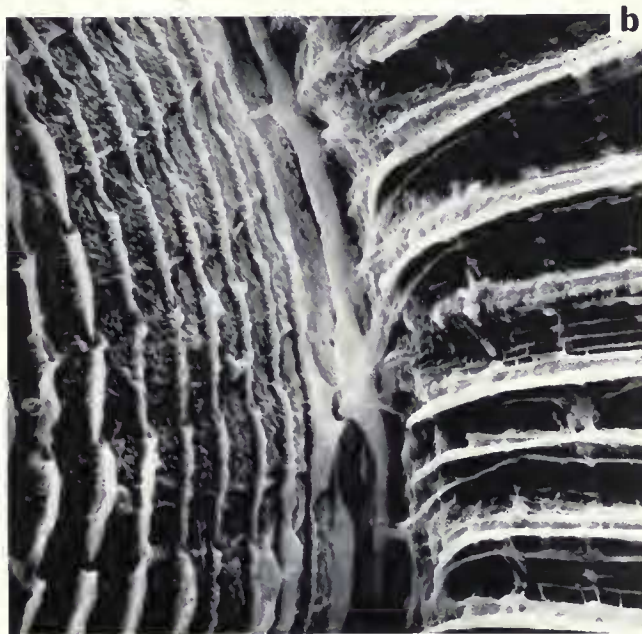
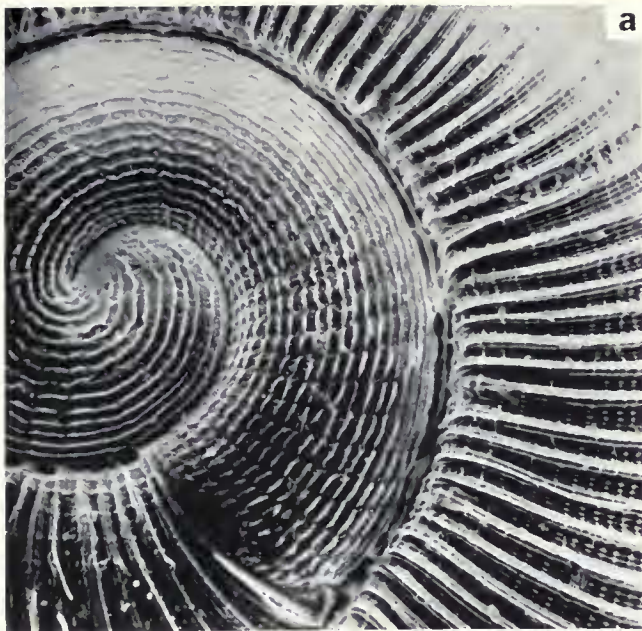


FIG. 4. Shell microsculpture in *Microcharopa mimula*. Central peak, Mothe, Lau Archipelago, Fiji. BPBM 78585: a, apex and part of 1st postnuclear whorl (295 $\times$ ); b, suture between apex and 1st postnuclear whorl (970 $\times$ ); c, center of apex (980 $\times$ ); d, center of apex (2,935 $\times$ ); e, detail of apical ridge (9,850 $\times$ ).



nents creating the visual effect requires 1,000× SEM viewing.

The transition between apical and postapical sculpture is quite abrupt (fig. 3d). There is a very short distance of stuttering apical growth, then a start of the typical postapical sculpture immediately. No differences in this pattern were seen in other species examined with the SEM.

Rib counts were made on the body whorl of all unworn adult specimens. The pattern of mean rib counts and rib spacing is presented in Table I and also discussed in the family comparison section. The question of the utility of rib counts is covered by Solem (1976b, pp. 39–44), and justification of this is not repeated here. Data on shell diameter and rib spacing correlations are presented in Table III. The correlation between shell diameter and rib spacing is less tight than in the Endodontidae (Solem, 1976b, p. 44, table XV), probably reflecting in part the smaller number of species involved. Rib reduction is discussed elsewhere (p. 9) and also is not as tightly correlated with size as in the Endodontidae (Solem, 1976b, pp. 47–50).

In the Endodontidae and the Charopidae there are a few situations in which the major ribs have become grossly enlarged and widely spaced. Although none of the charopids equals the spectacular "wings" of *Zyzyxonta alata* Solem (1976b, p. 466, fig. 198a–c), one does come close to the huge ribs of *Cookeconcha stellulus* (Gould, 1844) (Solem, 1976b, p. 218, fig. 93). *Palikirus cosmetus* (fig. 91d–f) from Ponape is the one example of spectacular rib enlargement in the Charopidae. Even when a keel is formed and the shell enlarged as in *Maafu thaumasius* (fig. 76a–c), the ribs themselves remain relatively small. When there is great size enlargement of the shell in such endodontid genera as *Gambiodonta* (Solem, 1976b, pp. 435–442, figs. 186–189), sometimes (*G. mirabilis* Solem, 1976; *G. grandis* Solem, 1976) there is clear rib enlargement.

Variation in the number of apical cords between charopid species is relatively small and generally is

greatly exceeded by the variation within species. A range of four to six within a population or species is not unusual where the mean is 11 or 12, dropping to a range of three to four where the mean is eight or nine cords. Such variation in part reflects accidents of post-nuclear whorl attachments that can change the count by one or two cords, which is partly what happens in terms of cord fragmentation near the upper suture and is partly actual variation in cord width and spacing. Because the intrapopulation variation is so large, little importance is attached to minor mean differences. Data on 83 of the 95 taxa were available. Of the remaining 12, *Discocharopa* has only radial apical sculpture, three had an apical sculpture too fine to count optically, five had the apex too worn, and three had the apical whorls missing or were worn fossils. Table I presents the dispersal of the species means, which shows a rather tight central cluster. Of the five species with a mean of less than 8.5 spiral cords, three (*Roimontis tolotomensis*, *Himeroconcha lamlanensis*, and *Kubaryiellus kubaryi*) have a moderately depressed to sunken spire, *Jokajdon callizonus* (Möllerndorff, 1900) (fig. 92a–c) may be involved in secondary size reduction, and only *Vatusila vaitupuensis* (fig. 85a–c) shows no special features explaining the reduction in number of apical cords. At the other extreme, *Lauopa mbalavuana* (fig. 77a–c) with 22 cords, *Microcharopa mimula* (fig. 4a) with a mean of 17.8, *Sinployea irregularis* (Garrett, 1872) (fig. 65d–f) with 18.5, *S. recurva* (fig. 64a–c) with 15.9, *S. angularis* (fig. 64d–f) with 14.6, and *Palline biakensis* (fig. 96a–c) with 14.0 cords show no clear indication of why the numbers have increased. Even the very elevated spire of *Ba humbugi* (fig. 74b) did not make a noticeable difference in apical cords (mean 12.0). The number is undoubtedly much higher in the species of *Tuimalila* (fig. 2c), but these cords are nearly suboptical in size and are partly obscured by the radial swellings.

Variation in the height of the apical cords can be studied easily with the SEM. A few examples are shown in Figures 1–3. The situation in *Sinployea modicella* (Férussac, 1840) is typical (fig. 1a–c), with the height of each cord (mean 9.2 cords) being slightly less than its width. There is an obscure radial rugosity as a secondary feature. Within the same genus, *Sinployea peasei* (fig. 2a–b) (mean 11.4 cords) shows a reduction in both height and width of each cord, although the underlying rugosity is just as clearly outlined. In *Tuimalila pilsbryi* (fig. 2c) the spiral cords are about the same size as in *Sinployea peasei*, but the secondary radial swellings confuse the viewer using optical equipment. Finally, in *Palline biakensis* (fig. 3a–d) the spiral cords are much higher and narrower, and there is no trace of the radial rugosities seen in the *Sinployea*.

Only two Pacific Island charopids show a different apical sculpture. *Microcharopa mimula* (fig. 4a–e) has spiral apical ribbing, but this is broken up into a series of short segments with peculiar open ends (fig. 4d–e).

TABLE III. - SHELL DIAMETER AND RIB SPACING IN THE CHAROPIDAE.

Ribs/mm.	Number of Taxa	Mean and Range of Shell Diameter in mm.
LESS THAN 2	2	6.06(4.59–7.52)
2.0–2.99	1	2.40
3.0–3.99	2	4.00(3.29–4.70)
4.0–4.99	5	4.88(3.49–5.68)
5.0–5.99	4	3.29(2.11–4.30)
6.0–6.99	6	3.45(2.17–5.23)
7.0–7.99	5	2.69(1.75–3.49)
8.0–9.99	14	3.06(1.65–4.63)
10.0–12.99	26	2.61(1.73–3.74)
13.0–19.99	14	2.29(1.40–2.95)
MORE THAN 20	6	1.91(1.07–3.21)

At optical magnifications the sculpture appears to be simple spiral cords, but obviously it is much more complex. The same sculpture is found in the North American *Radiodiscus millicostatus* (Pilsbry & Ferriss, 1906) (Solem, 1977b, p. 152, figs. 7–8) and an unnamed Western Australian genus (Solem, unpublished data). These genera are grouped in the charopid subfamily Rotadiscinae H. B. Baker (1927, p. 228). *Discocharopa aperta* (Möllerndorff, 1888) (fig. 5a–c) has an apical sculpture of fine radial ribs that become very crowded (fig. 5a) near the end of the apex. Higher on the apex (fig. 5b–c) there are irregularly spaced periostracal spiral folds that add a partial spiral element. The post-apical whorls (fig. 5d–f) show no trace of any spiral sculpture.

In summary, the Pacific Island Charopidae mostly have a very characteristic and conservative pattern of sculpture. The apex has a variable number of spiral cords to which radial swellings are occasionally added. The postapical whorls have major radials whose spacing and number are somewhat correlated with shell diameter, finer microradials in between, with very fine microspiral units that buttress or connect the microradials. Most of this sculpture is formed by the periostracum (p. 137). Reduction in prominence or loss of sculptural features is an apparently rare event.

The situation is much more complex in relation to the New Zealand and Australian charopid taxa.

#### APERTURAL BARRIERS

Traditionally, those endodontoid taxa with apertural barriers were placed in the form genus *Endodonta*, and those without barriers, in the form genus *Charopa* (Solem, 1976b, pp. 118–119). The discovery that taxa with apertural barriers showed family-level differences in anatomy is one of the more significant results of this study. Solem (1973b) reviewed the barrier frequency and structure in the two families and concluded that although the endodontoid barriers are of common origin, those found in the Pacific Island Charopidae have evolved at least four times. Thus, instead of considering monophyletic variation, as in the equivalent discussion of the endodontid barriers (Solem, 1976b, pp. 52–72), an obviously polyphyletic situation exists.

Such barriers are a common phenomenon in many land snail families (Solem, 1972c), but the timing of their appearance in ontogeny, methods of formation, state in adulthood of the individual, positions in the aperture, length, and numbers differ radically. They are analogous rather than homologous developments. Retention of specialized terms for the different structures found in separate families is fully justified. I have chosen to use a uniform terminology for the barriers in the Endodontidae and Charopidae, despite their independent origins, for ease in comparisons and because the barriers have the same patterns of change and growth. In both families the barriers appear at or

very shortly after hatching, are added to anteriorly and resorbed posteriorly during subsequent growth, and often effectively narrow the aperture in adulthood.

Recognition of parietal, columellar, and palatal zones in the aperture, the differences between major barriers and small traces, and the numbering sequence [parietals (upper to lower), columellars (upper to lower), palatals (lower to upper), all in numerical sequence *regardless of possible homology*] have been given by Solem (1976b, pp. 52–54, figs. 36–38).

The occurrence of barriers in the Charopidae is neither taxonomically nor geographically random: 32 (33.7%) of the 95 taxa have parietal and 27 (28.4%) have palatal barriers.<sup>1</sup> These are clustered in 11 of the 20 genera. *Lauopa*, *Discocharopa*, *Ladronellum*, and *Roimontis* are monotypic, *Jokajdon* and *Palikirus* have two species, *Graeffedon* and *Palline* have three, *Semperdon* has five, and *Lagivala* and *Vatusila* have six species. No species in these genera are without barriers, except for *Palikirus ponapicus* (Möllerndorff, 1900), which is known from a single, fungus-covered specimen and was associated with *Palikirus* as a convenience, and great secondary reduction of the barriers in *Vatusila niueana* (fig. 83e). Five of the 32 species are basically extralimital: *Lagivala macroglyphis* (Rensch, 1937) and *L. microglyphis* (Rensch, 1937) from New Britain; *L. demani* (Tapparone-Canefri, 1883) from Ambon, Timor, and parts of West Irian; *Palline biakensis* from West Irian; and *Discocharopa aperta* (Möllerndorff, 1888), which ranges from the Philippines to Society Islands. The three *Graeffedon* are limited to Western Samoa; the Lau Archipelago has two species (*Vatusila kondoi* and *V. nayauana*) on Nayau and *Lauopa mbalavuana* on Vanua Mbalavu and two species on Viti Levu (*Lagivala vivus* and *L. minusculus*). *Vatusila tongensis* on Eua, Tonga; *Lagivala davidi* (Ladd, 1968) fossil on Funafuti and *Vatusila vaitupuensis* live on Vaitupu, Ellice Islands; *V. niueana* on isolated Niue Island; and *V. eniwetokensis* (Ladd, 1958) fossil on Eniwetok in the Marshall Islands complete the western distribution. A second cluster of taxa occurs on some of the Caroline, Palau, and Mariana Islands. On Ponape there are *Palline micramyla*, *Jokajdon callizonus* (Möllerndorff, 1900), *J. tumidulus* (Möllerndorff, 1900), *Palikirus cosmetus* (Möllerndorff, 1900), and *Roimontis tolotomensis*. On the islands of Palau, the three subspecies of *Palline notera*, *Semperdon uncatus*, *S. xyleborus*, and *S. kororensis* (Beddome, 1889), are found. In the Mariana Islands *S. heptptychius* (Quadrass & Möllerndorff, 1894) and *Ladronellum mariannarum* (Quadrass & Möllerndorff, 1894) live on Guam, and *Semperdon rotanus* occurs on Rota and the northern tip of Guam.

<sup>1</sup>This differs from the figure cited by Solem (1973b, p. 301) because *Discocharopa aperta* (Möllerndorff, 1888) has some populations with and many without a parietal barrier, so this species was omitted from that calculation.



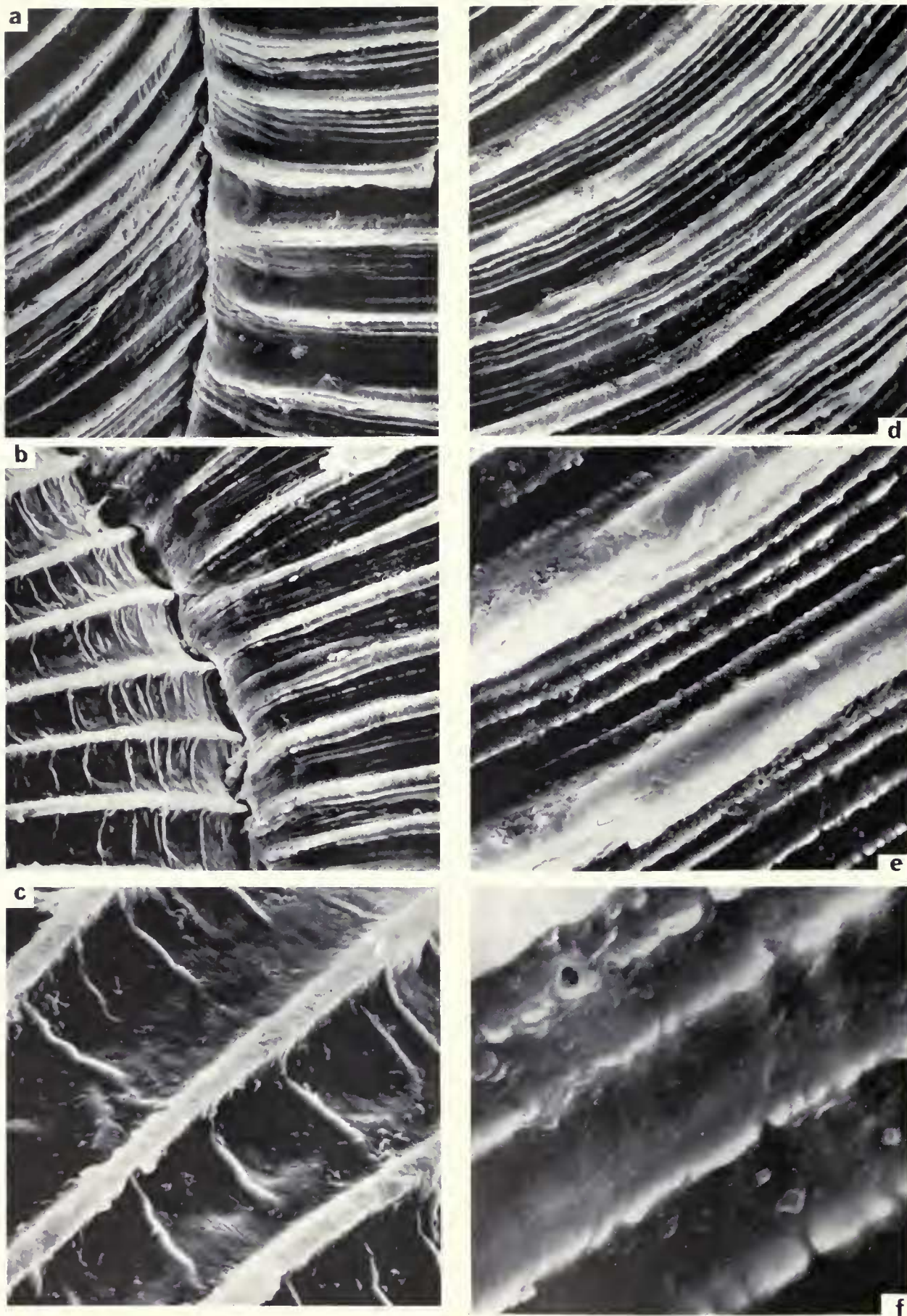


FIG. 5. Details of shell sculpture in *Discocharopa aperta* (Möllendorff). Busuanga, Philippine Islands. FMNH 18725: a, shell sculpture at apical-postnuclear boundary (1,000 $\times$ ); b, apical and postapical sculpture (1,035 $\times$ ); c, details of apical sculpture (3,000 $\times$ ); d, postnuclear sculpture (1,015 $\times$ ); e, postnuclear sculpture showing serrated edging (3,000 $\times$ ); f, detail of postnuclear sculpture showing absence of spiral elements (9,950 $\times$ ).



Except for the scattered occurrence of *Discocharopa aperta* (Möllerndorff, 1888) in the Austral Islands and on Borabora, Society Islands, the entire Cook and Society Islands area of great charopid diversity is free from barrier-bearing genera. Only the one taxon is known from Tonga, although several *Sinployea* and *Tuimalila* live in this group. Both the Lau Archipelago and Viti Levu have more taxa without than with barriers, as does Samoa. In Micronesia, Guam has the endemic barrierless *Himeroconcha*, and Ponape has two genera, *Kubaryiellus* and *Russatus*, that lack barriers. The Palau group is unique in having only barrier-equipped taxa in both the Endodontidae and Charopidae. On some other Caroline Islands, there are barrier-free taxa, and on both Funafuti and Vaitupu there are species of *Sinployea*. The extension of barrier-equipped taxa to the Marshall Islands represents their only penetration beyond the barrier-free taxa.

A summary of the evidence that the barriers in these genera represent independent derivations was given in Solem (1973b). The uniform pattern of microarmature and growth in the Endodontidae was reviewed both in Solem (1973b) and in more detail subsequently (Solem, 1976b, pp. 54–66, figs. 39–42). In brief, the tops of the endodontid barriers normally are modestly expanded into a cordlike shape, with very fine triangular points (Solem, 1976b, figs. 39e, 40, 41a–c, 42a–f) that are added to the surface. They are not parts of basic crystal layers that simply extend outward, but are an extra feature. Checking the resorption edge of a barrier (Solem, 1976b, p. 64, fig. 40) shows that they, at times, will be covered up by subsequent growth as the height of the barrier is increased.

The patterns in the Charopidae are only partly studied. At the time that most of the material used was on loan for study (1962–1967), the SEM was not yet available. In some of the genera, *Lagivala*, *Vatusila*, and *Graeffedon*, specimens are few in number and the barriers too deeply recessed for adequate SEM study without breaking the shell. Thus the following comments must be viewed as only introductory.

In *Jokajdon callizonus* (Möllerndorff, 1900) (fig. 6a–d) from Ponape, views of the third palatal barrier demonstrate the basic structures in one species complex. In vertical view of the posterior descending face, crest, and upper anterior descending face (fig. 6a), the etched resorption plane is on the left, whereas the right shows the larger platelets on the upper anterior slope of the barrier. At higher magnification (fig. 6b), the mixture of large and small platelets on the upper anterior face is seen in vertical view. In Figure 6d, the same area is shown in lateral view to demonstrate that the platelets are simply prolonged crystals from the growth face of the barrier. Figure 6c, at the point where the sharp anterior descension of the barrier ends, shows that there is an abrupt shift from large to small platelets. At this point, the combined major function of gripping surface for extending the body from the

shell aperture and providing setal catching projection against arthropod entry becomes much less significant, and hence the probable shift from large to small platelets.

Looking at the first palatal barrier in the Western Samoan *Graeffedon graeffei* (Mousson, 1869) (fig. 7a–c) shows a second pattern of structure. The specimen was taken alive, and the shell was partly fractured during dissection. The barrier surface was not worn, so that the structure of long, straight, projecting ridges across the anterior descending face of the barrier is normal. There is distinct variation in the length of the ridges (fig. 7b–c). The most intriguing aspect is seen on the side of the barrier (fig. 7a). The individual pockets hold platelets at a variety of angles, sometimes protruding, sometimes almost vertical in orientation. I consider it possible that they represent fragments from the adsorption surface that have been transported and re-fixed in a near anterior position. Unfortunately, specimens of *Graeffedon* are quite rare, and it is improbable that material sufficient to test this idea will become available for study.

The Palau Island *Semperdon xyleborus* (fig. 8a–e) has long parietal barriers, with the upper parietal posteriorly bifurcate (fig. 8a). The upper edge of the third parietal (fig. 8b–c) shows a few broad, projecting plates that point anteriorly. Some of them stretch across almost the entire edge. In lateral view (fig. 8d), the edge of the fourth parietal shows that the plates become much smaller on the side of the barrier and that the large plates are growing from the barrier surface as it slants slightly downward. They are partly elevated from the surface.

The basic difference between the three types can be summarized as: (1) crystal layers simply continued directly forward and broken into microplatelets (*Jokajdon*); (2) anterior added ridges that may be in part transported as large crystals (*Graeffedon*); and (3) broad ridges angled up from the surface layers (*Semperdon*). Despite similar appearance and function, these are actually three different ways of reaching the same end result, i.e., a series of microprojections that provide gripping surfaces for the advancing mantle collar during emergence of the body from a fully withdrawn position. They are just as effective as the fourth solution, the triangular points in the Endodontidae, but are not as elegantly constructed. Coupled with the very obvious size and position differences of the barriers in the three charopid examples cited, which are typical of their anatomical groupings, I conclude that they are of independent origin. When compared with the apertural barrier microstructure in other families (Solem, 1972c), the charopid experiments show greater individual variation and are much less “finished” in appearance, even though the use of angled plates is a more common pattern than the addition of points or barbs on the surfaces.

The presence of barriers in the Charopidae is a polyphyletic and secondary character, rather than the norm as in the Endodontidae. Thus, the comparative



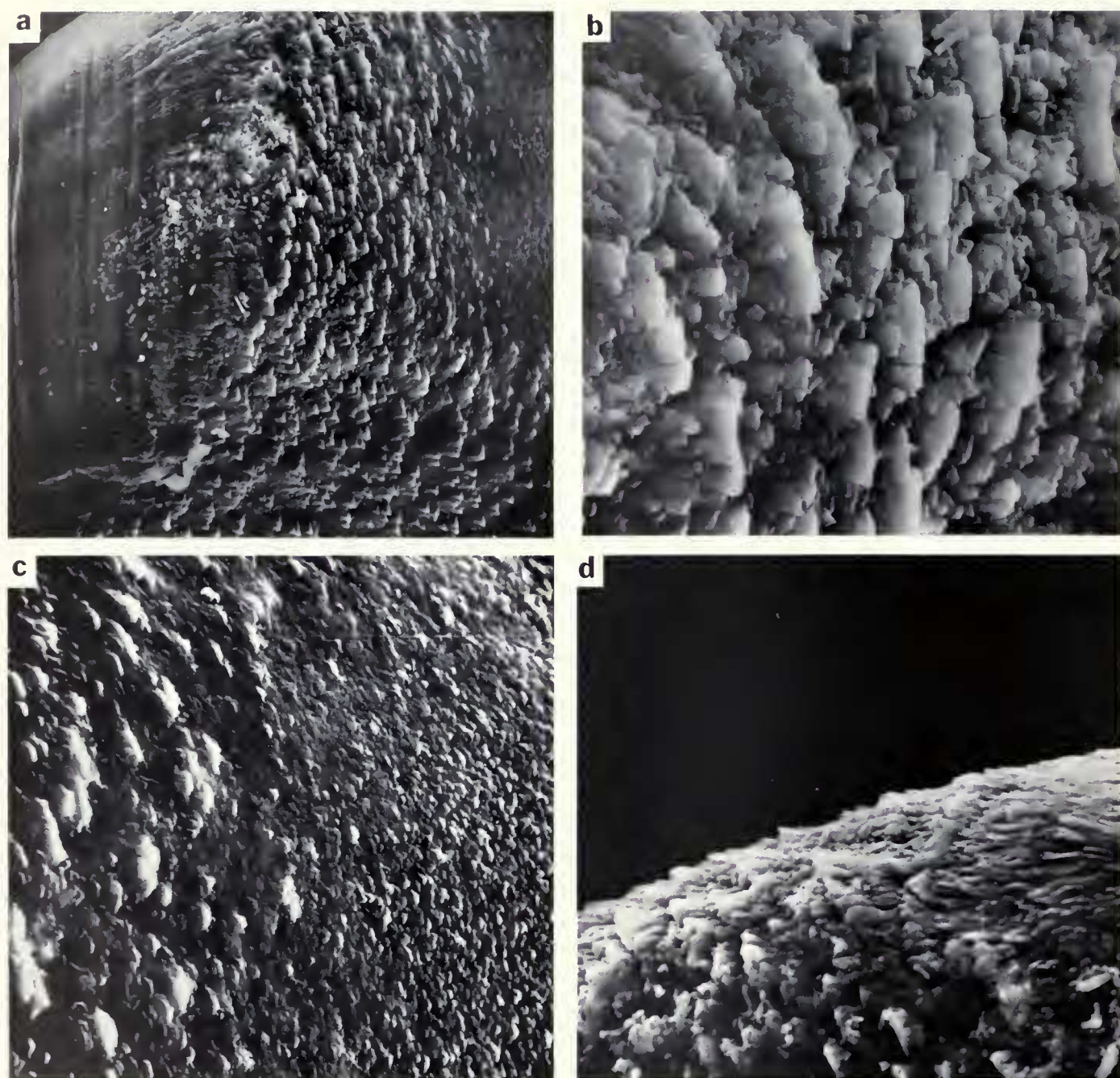


FIG. 6. Microstructure of largest palatal barrier in *Jokajdon callizonus* (Möllendorff). Station 118, Ponape, Caroline Islands. BPBM 154161: a, vertical view onto top of largest palatal at 1,030 $\times$ , note weak etch marks on upper left and the clear cross-strata pattern on entire posterior (left margin); b, area of sharp anterior slope in vertical view at 3,200 $\times$ ; c, area at bottom of sharp anterior descension showing transition from large crystal plates to small crystals at 3,125 $\times$ ; d, lateral view at 3,050 $\times$  of large crystal area showing how these plates are continuations of the vertical growth layers.

treatment will be different than in Solem (1976b). Correlations among barrier condition and other shell features are not as simple and direct as in the Endodontidae. For example, the relative degree of aperture narrowing in the Endodontidae (Solem, 1976b, p. 71, table XLVIII) and Charopidae (table IV) is quite different. The percentages of the barrier-possessing taxa that are intermediate in closure differ greatly. In the Endodontidae, 57.5% are intermediate, but only 25.0% in the Charopidae. The latter have the barriers

TABLE IV. - DEGREE OF APERTURAL NARROWING BY BARRIERS

	Endodontidae	Charopidae
Strong	19.9%	43.7%
Moderate	40.9%	9.4%
Weak	16.6%	15.6%
Not	22.6%	31.3%
Total Taxa	181	32



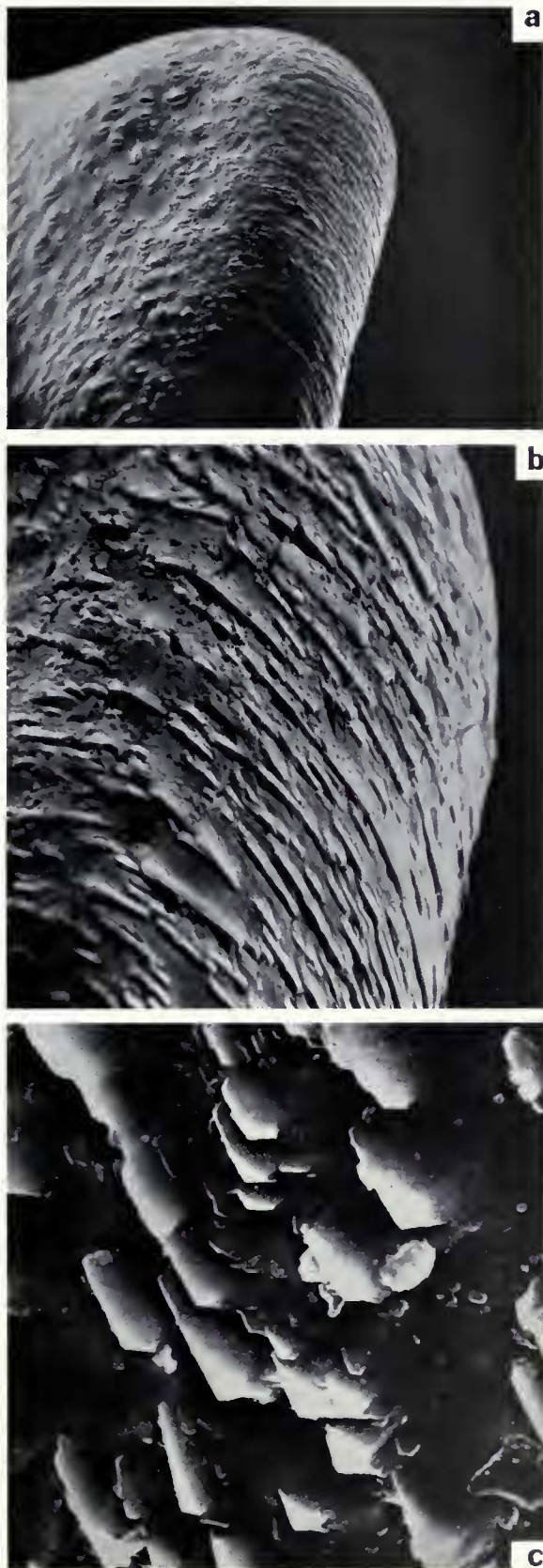


FIG. 7. Surface of largest palatal barrier in *Graeffedon graeffei* (Mousson). Station 39, Mt. Solaua, Upolu, Western Samoa. FMNH 153420. **a**, angled view of front edge and inner side showing different lateral and anterior surface texture (305 $\times$ ); **b**, anterior edge at 1,100 $\times$  showing projecting platelets on surface of descending edge; **c**, vertical view onto descending edge surface at 3,150 $\times$ .

either strongly constricting the aperture (figs. 98b, e, 99b, d, e), or they are essentially ridgelike remnants (figs. 85b, 101b).

In both families, more species have parietal barriers than either columellar and palatal, and no species has either of the latter without also having the former.

#### *Parietal barriers*

The number of parietal barriers ranges from the single barrier that may be present or absent in *Discocharopa*, to the four large barriers plus three traces found in *Semperdon xyleborus* (fig. 98e). The only variation in major barrier numbers occurs in *Semperdon heptptychius* (Quadras & Möllendorff, 1894), which normally has three parietals and one accessory trace. Occasionally (5.1%), the trace and third parietal are missing, rarely (0.3%), a fourth parietal is developed, and rarely (3.3%), the trace is missing. In *Semperdon xyleborus*, 84.6% have three traces, 15.4% have two traces. Occasionally, a parietal trace will be present in *Palline notera notera* and *P. n. gianda*, and there is one superior trace present in *S. rotanus* (fig. 99d). Otherwise, the number of parietal barriers is constant.

Barrier length partly correlates with height. The method of determining length is explained by Solem (1976b, p. 70, fig. 43). Where the parietal is a threadlike remnant, it is  $\frac{1}{6}$  to  $\frac{1}{8}$  whorl long (figs. 83e, 85b, 95d, 101b), except in *Palline biakensis* (fig. 96b) and *Roimontis tolotomensis* (fig. 91b) where the length reaches  $\frac{3}{16}$  of a whorl. In *Vatusila nayauana* (fig. 82e), *Semperdon uncatatus* (fig. 97b), and *Palikirus cosmetus* (fig. 91e), the parietal is a raised ridge, but still short. The only taxa with high, short barriers are the races of *Palline notera* (figs. 94b, e, 95a) and *Semperdon xyleborus* (figs. 8a, 98e). The remaining barriers are  $\frac{1}{4}$  to  $\frac{3}{16}$  of a whorl long, except for several species of *Lagivala* where they extend to or beyond the line of vision from the aperture (*L. microglyphis*, fig. 81b; *L. macroglyphis*, fig. 81e; *L. minusculus*, fig. 80e). These species are very small in size, with mean diameters of 1.55–1.73 mm.

Structure of the barriers is highly varied. The threadlike and raised ridge taxa present no unusual features and have been mentioned above. Where there is a single high barrier, such as *Lauopa mbalavuana* (fig. 77b), *Discocharopa aperta* (Möllendorff, 1888) (fig. 35a–b), and *Lagivala minusculus* (fig. 80e–f), it is a high thin blade, usually with abrupt anterior descension. When there are two or three high lamellae, the typical shape found in most of the Endodontidae is usual: an abrupt posterior resorption face, elevated middle with slightly to strongly expanded upper edge, and then gradual anterior descension. The second and fourth parietals in *Semperdon xyleborus* (fig. 8a) are typical. Several taxa have a modification of the first parietal that also was found in some Endodontidae. It can become deflected downward on the posterior portion in *Jokajdon callizonus* (Möllendorff, 1900) (fig. 92b), *Semperdon heptptychius* (Quadras & Möllen-



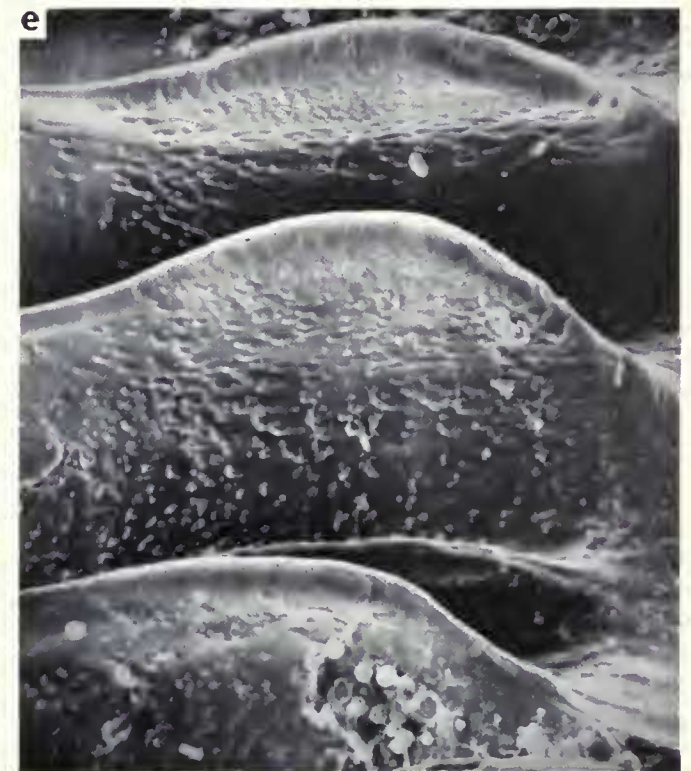
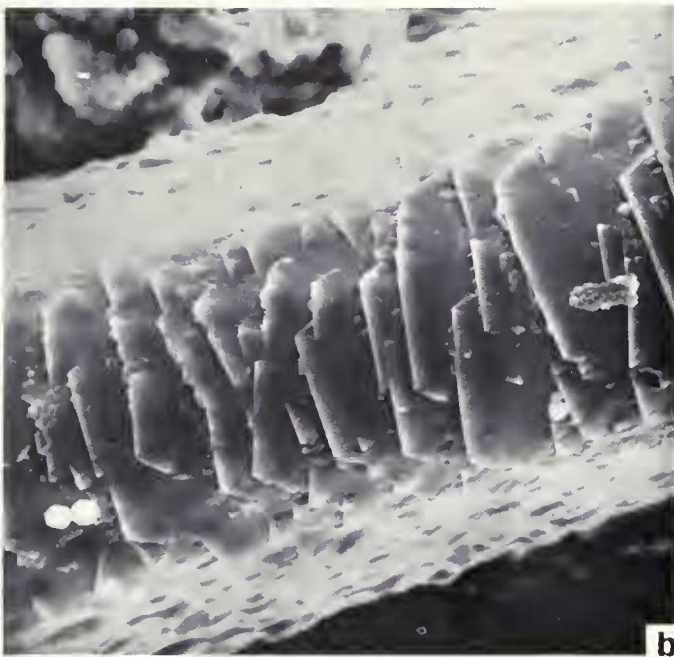
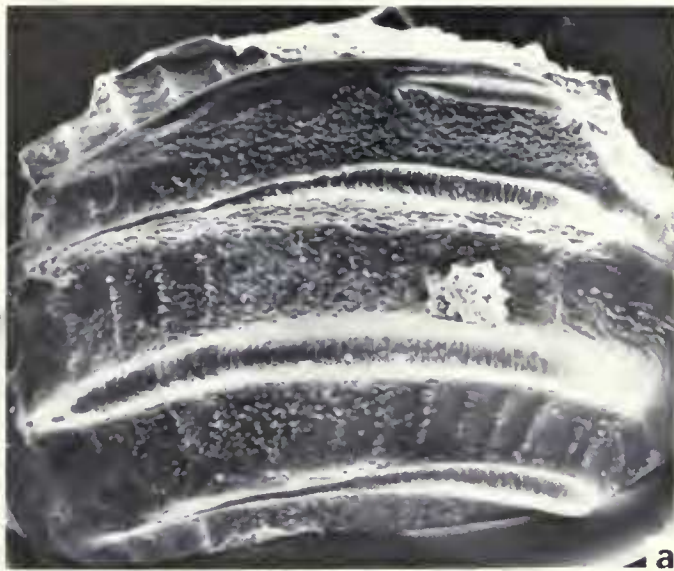


FIG. 8. Structure of apertural barriers in *Semperdon xyleborus*. Station 184, Peleliu, Palau Islands: a, parietal barriers at 120 $\times$ , note posterior bifidity of upper (1st) parietal; b, upper edge of 3rd parietal at 950 $\times$ ; c, upper edge of 3rd parietal at 2,850 $\times$ ; d, upper edge of 4th parietal at 2,910 $\times$ ; e, lower palatal barriers at 326 $\times$ . Anterior side at left margin in each photograph.

dorff, 1894) (fig. 99b), and *S. rotanus* (fig. 99d); it is bifid in *Vatusila tongensis* (fig. 83b) or posteriorly bifurcated in *V. kondoi* (fig. 82b), *Jokajdon tumidulus* (Möllendorff, 1900) (fig. 92e), *Semperdon kororensis* (Beddome, 1889) (fig. 98b), and *S. xyleborus* (fig. 8a, upper barrier). Similar bifurcation was found also in three lineages of the Endodontidae—several *Cookeconcha* and *Endodonta* (Solem, 1976b, p. 379, fig. 167a, g), some *Minidonta* (Solem, 1976b, p. 138, fig. 65b,d–e, g; p. 149, fig. 71c), and some *Anceyodonta* (see Solem, 1976b, p. 57). The reason for these repetitive bifurcations, usually of the upper parietal barrier, is unknown.

The basic similarity in shape between the larger parietals of the Charopidae and Endodontidae probably indicates that this is an efficient shape, not only in terms of continual anterior addition and posterior resorption, but also in functioning during body extension of the animal.

None of the Charopidae show the splitting into threadlike traces of the barriers that was common in several lines of the Endodontidae (Solem, 1976b, p. 57; p. 332, fig. 144a–c).

The Charopidae show instead a quite conservative shape and number pattern of the parietal barriers.

#### Columellar barriers

Of the 32 taxa with parietal barriers, 13 lack any columellar barrier. This part of the shell is missing in *Vatusila eniwetokensis* (Ladd, 1958), so that its situation is unknown. *Semperdon xyleborus* and *S. kororensis* (Beddome, 1889) (fig. 98b–c, e) have two prominent columellar barriers, and the former species normally has two accessory traces above the upper columellar. Six taxa, *Lagivala macroglyphis* (Rensch, 1937) (fig. 81e–f), *L. microglyphis* (Rensch, 1937) (fig. 81b), *Jokajdon callizonus* (Möllendorff, 1900) (fig. 92b), *J. tumidulus* (Möllendorff, 1900) (fig. 92e–f), *Graeffedon savaiiensis* (fig. 88b), and *Palline notera notera* (fig. 94b) have only one columellar. This varies from a threadlike ridge in the last two, to high and sometimes sharply ascending barriers in the other four species. The remaining 10 taxa (table V) show intraspecific variation in the number or absence of columellar barriers. When the variation is present or absent, in all but *Lagivala demani* (Tapparone-Canefri, 1883), the barrier is minute and threadlike. Its absence would mostly result from being covered by the basal callus. In *Lagivala demani* (Tapparone-Canefri, 1883) the variation is geographic, with a large columellar present in specimens from Timor, medium-sized in Ambon and Aru Islands shells, and very small to absent in Biak and West Irian examples. In *Semperdon rotanus* and *S. heptapychius* (Quadras & Möllendorff, 1894) (fig. 99e) the second columellar, when present, is a small threadlike trace above the larger columellar that is a high ridge parallel to the plane of coiling. A large form of the latter species (fig. 99b) occurs in which the columellar barrier is absent.

TABLE V. – PERCENTAGE DISTRIBUTION OF COLUMELLAR BARRIER NUMBERS.

Taxon	Number of Columellar Barriers			
	0	1	2	3
<i>Vatusila kondoi</i>	5.6	94.4		
<i>V. nayauana</i>	40.0	60.0		
<i>Lagivala demani</i>	*	*		
<i>Graeffedon graeffei</i>	30.0	70.0		
<i>Palline notera gianda</i>	84.0	16.0		
<i>P. notera palauana</i>	95.0	5.0		
<i>Semperdon uncatus</i>	83.0	17.0		
<i>S. rotanus</i>		46.5	53.5	
<i>S. heptapychius</i>	0.3	42.1	56.4	1.2
<i>Ladronellum mariannarum</i>	3.5	96.5		

\* Geographically variable.

In most taxa the columellar barrier lies parallel to the plane of coiling. *Semperdon xyleborus* and *S. kororensis* (Beddome, 1889) have one barrier slanting downward (fig. 98b, e); *Jokajdon tumidulus* (Möllendorff, 1900) (fig. 92e), *Lagivala microglyphis* (Rensch, 1937), and *L. macroglyphis* (Rensch, 1937) (fig. 81b, e–f) have it twisted up toward or almost onto the parietal wall; and in others, such as *Jokajdon callizonus* (Möllendorff, 1900) (fig. 92b), it is a deeply recessed, triangular knob.

Thus, the 18 species of Charopidae known to have a columellar barrier show almost the same total range of variation reported for the Endodontidae (Solem, 1976b, pp. 57–59).

#### Palatal barriers

Five of the 32 taxa with parietal barriers lack palatals—*Lauopa mbalavuana* (fig. 77b), *Discocharopa aperta* (Möllendorff, 1888) (fig. 36b), *Palline biakensis* (fig. 96b), *Roimontis tolotomensis* (fig. 91b), and *Palikirus cosmetus* (fig. 91e). Except for the *Roimontis*, which has two threadlike parietals, all of them have only a single, short lamellar parietal. Because of the missing palatal wall in the holotype and only known example, the palatal barrier situation in *Vatusila eniwetokensis* (Ladd, 1958) is unknown. In *Ladronellum mariannarum* (Quadras & Möllendorff, 1894) (fig. 101b), many *Vatusila nayauana* (fig. 82e), and *V. niueana* (fig. 83e) there is a modest ridge to barely detectable trace on the middle of the palatal wall. *Semperdon uncatus* (fig. 97b) normally has one low barrier on the basal lip, but in 17% of the individuals this is missing, and *Palline micramyla* (fig. 95d) has two low lamellar barriers on the basal lip. *Lagivala minusculus* (fig. 80e) has a rather unique ridge with a lateral buttress on the basal lip, and *Vatusila tongensis* (fig. 83b) has a very large basal lip barrier that is bifurcated or split into two parts plus a very unusual



upper raised callus that is 0.25–0.36 mm. wide. *Vatusila vaitupuensis* (fig. 85b) has a midpalatal thread-like trace and a broader ridge on the basal lip very near the columellar margin.

The remaining species have a more typical array of normally three to seven palatal barriers, sometimes with additional accessory traces present. The positioning of these barriers varies from at the lip edge in *Semperdon* (figs. 98b–c, e, 99b, d, e), *Palline notera* and its subspecies (figs. 94b, e, 95a), *Graeffedon* (figs. 88b, e, 86b), and *Lagivala microglyphis* (Rensch, 1937) (fig. 81b), to partly recessed in *Jokajdon callizonus* (Möllendorff, 1900) (fig. 92b), progressively recessed in *J. tumidulus* (Möllendorff, 1900) (fig. 92e), moderately recessed in *Vatusila kondoi* (fig. 82b) and *Lagivala macroglyphis* (Rensch, 1937) (fig. 81e), and deeply recessed in both *L. vivus* (fig. 80b) and *L. davidi* (Ladd, 1968) (Ladd, 1958, pl. 30, figs. 13–15).

The shape of the barriers is rather variable among these species, although constant within a particular species. A simple crescent-shape with modestly to moderately expanded upper edge is found in *Lagivala vivus* (fig. 80b), *L. macroglyphis* (Rensch, 1937) (fig. 81e), and *L. demani* (Tapparone-Canefri, 1883); a more expanded upper edge, in *L. microglyphis* (Rensch, 1937) (fig. 81b) and *Graeffedon pricei* (fig. 88e); typical structure, in *Vatusila kondoi* (fig. 82b); very high, in *Graeffedon graeffei* (Mousson, 1869) (fig. 86b) and *G. savaiiensis* (fig. 88b); typical, in the races of *Palline notera* (figs. 94b, e, 95a); and bulbous-edged, again in *Semperdon rotanus* and *S. heptapytychius* (Quadrass & Möllendorff, 1894) (fig. 99b, d–e). In *Semperdon xyleborus* (figs. 8e, 98e), the crescent is anteriorly elongated, a process continued in the two species of *Jokajdon* (fig. 92b, e,) and reaching the typical parietal barrier shape in *Semperdon kororensis* (Beddome, 1889) (fig. 98b).

The predominance of the crescent-shaped palatal barriers outlined above is very different from the situation in the Endodontidae. In that family (Solem, 1976b, p. 60, table XXXII) only five species had crescentic palatals, whereas 130 had bladeliike barriers. In the Charopidae, only the two *Jokajdon*, *Semperdon kororensis* (Beddome, 1889), and possibly *S. xyleborus* could be considered to have a bladeliike palatal barrier form.

Intraspecific variation in the number of palatal barriers is summarized in Table VI. The great variation found in the two *Semperdon* exceeds that found in any of the Endodontidae (Solem, 1976b, p. 67, table XL). None of the ratios in Table VI convincingly suggests genetic dominance. Assigning the most frequent percentage to represent that species, the pattern of palatal barrier numbers is summarized in Table VII. It is evident that there is considerable variation within genera, particularly *Lagivala*, *Graeffedon*, *Palline*, and *Semperdon*. Even within genera, there is no clear correlation between number of barriers and shell size. Only *Palline notera* shows a partial correlation, in that the two larger subspecies have fewer and smaller-sized

TABLE VI. - PERCENTAGE DISTRIBUTION OF PALATAL BARRIER NUMBERS

Taxon	Number of Palatal Barriers									
	0	1	2	3	4	5	6	7	8-10	
<u>Vatusila kondoi</u>			11.1	88.9						
<u>V. nayauna</u>	40.0	60.0								
<u>Lagivala demani</u>	*			*	*					
<u>Graeffedon graeffei</u>					20.0	80.0				
<u>Palline notera palauana</u>				10.0	75.0	10.0	5.0			
<u>P. n. gianda</u>				16.0	68.0	16.0				
<u>Semperdon uncatus</u>	17.0	83.0								
<u>S. rotanus</u>					1.2	3.0	19.8	55.0	21.0	
<u>S. heptapychius</u>				1.2	80.0	13.1	3.9	1.5	0.3	
<u>S. xyleborus</u>								92.0	8.0	

\* Geographically variable.

palatals than the nominate race, which averages 0.24–0.41 mm. less in diameter than the others. There is also no clear correlation between number of palatals and degree of apertural narrowing.

The presence of palatal traces is sporadic. Several taxa will have one or two traces between lower pairs of palatal barriers: *Lagivala microglyphis* (Rensch, 1937), *Graeffedon graeffei* (Mousson, 1869), *G. pricei*, *Palline notera gianda*, *Semperdon rotanus*, and *S. heptapytychius* (Quadrass & Möllendorff, 1894). Other taxa will have three traces above the upper palatal: *Jokajdon callizonus* (Möllendorff, 1900), *Semperdon kororensis* (Beddome, 1889), and most examples of *S. xyleborus*. A few of the latter will have four (7.5%) or five (7.5%) traces above. *Jokajdon tumidulus* (Möllendorff, 1900) normally has three traces above the upper palatal and three (rarely two) between lower pairs. The same pat-

TABLE VII. - PALATAL BARRIER NUMBERS IN CONSTRICTED APERTURE CHAROPIDAE.

3 Palatals	5 Palatals
<i>Vatusila kondoi</i>	<i>Lagivala microglyphis</i>
<i>Lagivala demani</i>	<i>L. macroglyphis</i>
<i>Jokajdon callizonus</i>	<i>Graeffedon graeffei</i>
<i>J. tumidulus</i>	<i>Palline notera notera</i>
4 Palatals	6 Palatals
<i>Lagivala davidi</i>	<i>Lagivala vivus</i>
<i>Graeffedon pricei</i>	
<i>Palline notera gianda</i>	7 Palatals
<i>P. n. palauana</i>	<i>Graeffedon savaiiensis</i>
<i>Semperdon heptapytychius</i>	<i>Semperdon rotanus</i>
	<i>S. xyleborus</i>
	<i>S. kororensis</i>

tern of traces above the upper palatal is seen in the Endodontidae (Solem, 1976b, p. 59) and was interpreted as a space-preserving function, because the great size of the first parietal and the need to keep this space open for withdrawal and extension of the buccal mass and foot combine to make reduction in size of palatal projections in this area advantageous.

As in the Endodontidae, the normal pattern of size change is for the palatal barriers to decrease in height as they ascend the palatal wall. An obvious exception will be reduced size of the first palatal in situations where it is right at the columellar margin (fig. 99d) or where there is large size to the columellar and/or lower parietal barriers (figs. 86b, 92b, e). So few taxa show either recession of the palatals or major upper edge expansion of the barriers that discussion of shell correlations separately is not attempted. Most of the comments made about general features of the palatal barriers in the Endodontidae (Solem, 1976b, pp. 59–63) seem to apply to the few Charopidae also.

Despite only 27 charopids having palatal barriers, they show a wide range of variations that mostly parallel the situations found in the Endodontidae. The biggest difference lies in the basic shape of the barriers: bladelike in 86.1%, ridged in 10.6%, and crescent-shaped in 3.3% of those Endodontidae with palatal barriers compared with bladelike in 15.4% (four), a lamellar or unusual ridge in 23.1% (six), and crescent-shaped in 61.5% (16) of the 26 charopid taxa for which data on the palatal barrier structure were available. Judging from the size of the parietal barriers (fig. 85e), *Vatusila eniwetokensis* (Ladd, 1958) probably had large palatal barriers, but the entire outer wall of the only known specimen is missing, and thus the state of the barriers is unknown.

#### *Patterns of barrier variation*

Despite the lack of size and shape correlations with variation in the barriers found in the Charopidae, a few comments can be made concerning general patterns within a particular group. In *Lagivala* (figs. 80–81) the variation is geographic, with the Bismarck Archipelago species having the strongest apertural barriers, progressive reduction occurring in both *L. demani* (Tapparone-Canefri, 1883) to the west and in the Fijian and Funafuti taxa to the east (fig. 80b, e). *Vatusila* shows no size correlation, with the largest (*V. tongensis*, fig. 83b) and one of the smaller (*V. eniwetokensis*, fig. 85e) having quite large barriers, and both large (*V. vaitupuensis*, *V. niueana*, figs. 83e, 85b) and small (*V. nayauana*, fig. 82e) having reduced barriers. There does appear to be some geographic concordance, with Tonga and Lau species having larger barriers than taxa from the more isolated Vaitupu and Niue localities. The fossil record of a large-barriered form on Eniwetok in the Upper Miocene gives an historical perspective to the group that otherwise is lacking in the Charopidae.

The reasons for the reduction in barrier size in the

races of *Palline notera* on Koror (*palauana*, fig. 94e) and Babelthuap (*gianda*, fig. 95a) compared with the nominate race on Peleliu (fig. 94b) is unknown, although slight size differences are involved. Barrier size variation in *Semperdon* shows no correlations that I could detect. The unconstricted aperture of the mean diameter 2.83 mm. *S. uncatus* (fig. 97b) contrasts with the highly constricted aperture in the mean diameter 2.88 mm. *S. xyleborus* (fig. 98e) and mean diameter 4.59 mm. *S. kororensis* (Beddome, 1889) (fig. 98b). All of these species have been dissected and all occur on Koror. The differences in barrier prominence cannot be explained at present.

#### *Summary of barrier variations*

Despite the different microstructure on the barrier edges and the evident polyphyletic origin of the apertural barriers in the Charopidae, in general they parallel those of the Endodontidae. The retention of parietal barriers extending to the lip edge, general shape, and multiple bifurcations of the parietals all suggest parallel function. Given the similar habitat and overlapping shell size, plus the same basic growth structure, this is not surprising. The difference in shape frequency of the palatal barriers, a greater tendency for loss or reduction in the barriers, and the general shorter length of the charopid barriers are real average differences but cannot be used as criteria for family-level separation because there is so much overlap between families.

#### SUMMARY OF SHELL VARIATIONS

With few exceptions the range of variation in the shells of the Charopidae is less than that found in the Endodontidae. Major differences between the two families are reviewed on pp. 40–44. Here it is sufficient to point out that the formation of sculpture by the periostracum rather than the calcareous layers, lack of umbilical and growth modifications to form a brood chamber, and secondary derivation of apertural barriers in the Charopidae have had profound effects on the range of shell variation.

#### GROSS ANATOMY

Including the *Punctum* sp. from Tahiti, *Sinployea* sp. from Borabora, and *Sinployea* sp. from Saipan, there are 98 species-level taxa considered in this monograph. Of these, 51 (52.0%) belong to one genus, *Sinployea*. It was possible to see at least fragmentary soft parts for 43 (43.9%) of the total taxa and 21 (41.1%) of the *Sinployea*. The taxonomic distribution of the dissected material is given in Table VIII. Of the 21 genera, six genera, five of them monotypic, could not be dissected. Only *Lagivala*, with six species, represents an undissected speciose group. The taxonomic coverage of dissected material is broader than that given the Endodontidae (Solem, 1976b, p. 73, table L), where only 58 (32.4%) of the 179 taxa seen were dissected. This reflects both a lesser degree of extinction for the



TABLE VIII. - PHYLETIC REPRESENTATION OF DISSECTED TAXA.

	Total Taxa	Number Dissected
Family Punctidae		
<u>Punctum</u>	2	-
Family Charopidae		
<u>Discocharopa</u>	1	1
<u>Microcharopa</u>	1	-
<u>Sinployea</u>	51	21
<u>Ba</u>	1	1
<u>Maafu</u>	1	-
<u>Lauopa</u>	1	-
<u>Tuimalila</u>	2	1
<u>Lagivala</u>	6	-
<u>Vatusila</u>	6	1
<u>Graeffedon</u>	3	1
<u>Trukcharopa</u>	1	1
<u>Kubaryiellus</u>	1	1
<u>Russatus</u>	1	1
<u>Roimontis</u>	1	-
<u>Palikirus</u>	2	1
<u>Jokajdon</u>	2	2
<u>Palline</u>	5	2
<u>Semperdon</u>	5	5
<u>Ladronellum</u>	1	1
<u>Himeroconcha</u>	4	3
TOTALS	98	43

Charopidae and a difference in areas of species abundance.

In part, the apparent greater amount of anatomical data for the Charopidae is illusory because many taxa were represented only by pulled fragments. This reflects the method of processing and specimen storage used at the BPBM (see Solem, 1976b, p. 19). Most frequently, a break occurs so that the digestive gland and ovotestis do not pull out of the shell, but sometimes only the head and terminal genitalia will be extracted. Thus, in only 21 of the 43 taxa do I have data on the ovotestis structure. For 14 additional taxa I could record data on the postapical genitalia and the entire pallial region. For four taxa most of the terminal genitalia was extracted, but only part or none of the pallial region, and for four taxa it was possible to record data on penial structure only. Only partial review of the anatomical patterns is possible.

The sequence of discussion follows that used for the Endodontidae (Solem, 1976b, pp. 72-99). Explanations and data presented there are not repeated, although fully cross-referenced. In certain cases, reference is made to extralimital taxa that have bearing on subfamily assignments. Where appropriate, their anatomy is illustrated here to provide standards against which to measure the variations found in the Pacific Island taxa. Illustration of the anatomy for new Australian and Lord Howe Island taxa will be presented elsewhere, although data from them are used to establish subfamily limits.

## GENITAL SYSTEM

The organs are discussed in approximate order from apex of the coiled visceral hump to the atrium. The terminology is modified from that originated by H. B. Baker (1938b, pp. 6-10, 92) and follows exactly the usage in Solem (1976b) with a few additions for new structures.

**OVOTESTIS (G)**—The hermaphroditic gland or ovotestis in the Charopidae normally consists of one or two clumps of palmately clavate alveoli that usually lie buried in the digestive gland above the stomach-intestine junction. The only Pacific Island species that departs from this pattern is *Discocharopa aperta* (Möller-endorff, 1888) (fig. 34a), where the bilobed ovotestis (G) lies alongside the stomach rather than apically in the digestive gland. In *Sinployea* (figs. 39b, g, 43c, 53g, 57b, 60b) there may be one or two lobes, basically depending on exactly where the last branching of the hermaphroditic duct occurs. Generally the branching of the ducts is simple, but in *Graeffedon graeffei* (Mousson, 1869) (fig. 87d) there are lateral short branches off the individual alveoli after the initial bifurcation. In *Ba humbugi* (fig. 75c) the ovotestis is shortened considerably. *Jokajdon*, *Kubaryiellus*, and *Ladronellum* have one clump, *Palline* and *Trukcharopa*, two clumps—typical differences are seen in Figure 90f, i. Species of *Semperdon* (fig. 100c, g) have one or two clumps. In every case these clumps lie essentially parallel to the plane of coiling and extend apically with only an initial angling outward from the parietal wall where the start of the hermaphroditic duct lies.

This is a very different pattern from the perpendicular to slanted orientation and division into a larger number of lobes seen in the Endodontidae (Solem, 1976b, p. 74, fig. 44). Similar orientation and multiplication of ovotestis lobes is found in some Australian and New Zealand Charopidae, but among the Pacific Island Charopidae and Endodontidae genera the ovotestis differences are diagnostic.

**HERMAPHRODITIC DUCT (GD)**—As in nearly all pulmonates, this duct serves to transport sex products from the mass of the ovotestis to the fertilization area below the expanded stomach. Its length is directly correlated with the length of the stomach, which, in turn, is dependent upon the whorl count and cross-sectional whorl area in this part of the visceral hump. In *Ba humbugi*, which averages only 3% whorls and has a comparatively wide aperture (fig. 74b), the hermaphroditic duct (fig. 75c) is very short compared with most other taxa. Whether the ovotestis starts after union of the ovotestis collecting tubules with a sudden or gradual expansion appears to be possibly seasonal. In no species did I have samples from the same population taken in different months of the year available in order to check whether swelling is a sign of reproductive activity. None of the Charopidae show the "kinking" of the hermaphroditic duct seen in the Endodont-

idae (Solem, 1976b, p. 75, fig. 45). The charopids do show a characteristic purple-red, iridescent sheen to the hermaphroditic duct that is not seen in the endodontids.

**TALON (GT) and CARREFOUR (X)**—The talon (GT) varies from a simple swelling just above the entrance of the hermaphroditic duct (GD) (fig. 39e) to a circular head on a stalk (fig. 103e). The carrefour (X) is a slight swelling in the tract after reflexion of the duct. The same pattern holds in all the species examined from the Pacific Islands. As usual in both the Charopidae and Endodontidae, there is a partial reflexion of the hermaphroditic duct before it enters the carrefour. This permits the compaction of apical organs when the animal has retracted into the shell. The general pattern of a circular head on a short stalk in the Pacific Island charopids contrasts with the more slender head pattern in the endodontids (Solem, 1976b, p. 85, fig. 49a; p. 373, fig. 164b; p. 471, fig. 199c), but the differences are small in many cases, and the variation in extralimital charopids is extensive. In both families the collecting ducts of the albumen gland empty into the carrefour below the level of the hermaphroditic duct entrance (fig. 39e; Solem, 1976b, p. 471, fig. 199c). No histological studies have been made of structures in this area.

**ALBUMEN GLAND (GG)**—The distance between the apex of the pallial cavity and the base of the stomach is less in the Charopidae than in the Endodontidae, since the median whorl counts are, respectively,  $4\frac{1}{8}$ — and  $5\frac{1}{2}$ +. In the Endodontidae, there is more of a tendency for the albumen gland to be elongated and to occupy only part of this area. In the Charopidae, the albumen gland is almost shapeless, roughly globular, with the surface deeply indented by intestinal loops, head of the spermatheca (S), esophagus, arteries, and stomach base. Rarely does the albumen gland dissect out intact, and in order to check the shape of the talon and carrefour plus the point of entrance for the hermaphroditic duct, some of the albumen gland tissue has to be teased away before illustration. Thus, only rarely can the actual shape be shown. The size of the alveoli appears larger in the Charopidae than in the Endodontidae, but no quantification of this was attempted.

**PROSTATE (DG) and UTERUS (UT)**—In the Endodontidae (Solem, 1976b, pp. 77–78; p. 373, fig. 164d; p. 471, fig. 199c) the prostate and uterus are completely separate tubes that are only lightly bound together by connective tissue. In the Charopidae they are partly (some Rotadiscinae) to completely (most Charopinae) fused, sharing a common lumen, with the prostate channel a lateral outpocket (fig. 102e) into which enter the prostatic alveoli. These are much fewer in number than in the Endodontidae, longer, and not arranged in distinct rows. Generally the prostate is as long as the expanded uterine upper section and extends slightly down along the even more expanded uterine lower

chamber. The latter tapers into the free oviduct (UV) without clear demarcation, so the exact relationship between prostate and uterine length remains to be determined by histological studies.

The uterus has a clear separation into an upper (UT<sup>1</sup>) thin-walled narrower chamber and a lower (UT<sup>2</sup>) thick-walled, more expanded chamber (fig. 43c–d). Presumably, actual egg encapsulation takes place in the lower chamber. This is simpler than the situation in the Endodontidae (Solem, 1976b, p. 449, fig. 191b) where four sections could be distinguished in the uterus. Comparative studies on the function and histology of this area in both families would be quite worthwhile. Solem (1972b, pp. 108–112) reviewed the pattern of fused versus separated pallial gonoducts in the Pulmonata and concluded that the separated condition found in the Endodontidae was more primitive than the fused condition found in the Charopidae and many European-North American families.

**TERMINAL MALE GENITALIA**—The organs that may be present in this complex are the vas deferens (VD), epiphallus (E), penial retractor muscle (PR), penis (P), penis sheath (PS), atrium (Y), and internal structures of the epiphallus and penis proper. The latter regions are used in species recognition by the snails, so that highly significant variations can be found within genera, particularly under conditions of sympatry. The discussion of variations in the Endodontidae (Solem, 1976b, pp. 78–83) should be read as background information on the general patterns before attempting to deal with the complexities in the Charopidae, where few of these organs are constant in shape.

The vas deferens (VD) starts from the end of the prostate alveoli attachment and tapers for a variable distance before becoming a narrow tube that reflexes at the penioviducal angle to ascend the penis. The area of tapering can be very short as in *Russatus* (fig. 90b), long in *Ladronellum* (fig. 102a), extend nearly to the penioviducal angle as in *Tuimalila* (fig. 79b), or highly variable as in *Sinployea* (fig. 67a, e–f, h). The ascending arm of the vas deferens is without unusual features until it reaches the next structure, which differs from subfamily to subfamily of the Charopidae.

In the Charopinae the vas deferens (VD) passes into an epiphallic enlargement that may be apical or anterior of the penial retractor muscle insertion. In *Charopa coma* (Gray, 1843) (figs. 9b, d, 10) there is an enlargement of the vas deferens about one-third of the way from the penial retractor muscle insertion. Internally (fig. 10) it can be seen that the actual differentiation occurs some distance after the swelling has begun. Internal pilasters of the vas deferens (VD) enlarge, terminating in finger-like projections that surround a central cavity. Below this point, which is the start of the epiphallus, two high pilasters and a lower ridge line the inside of the epiphallic chamber down to the point of entry into the penis chamber (fig. 9d). The



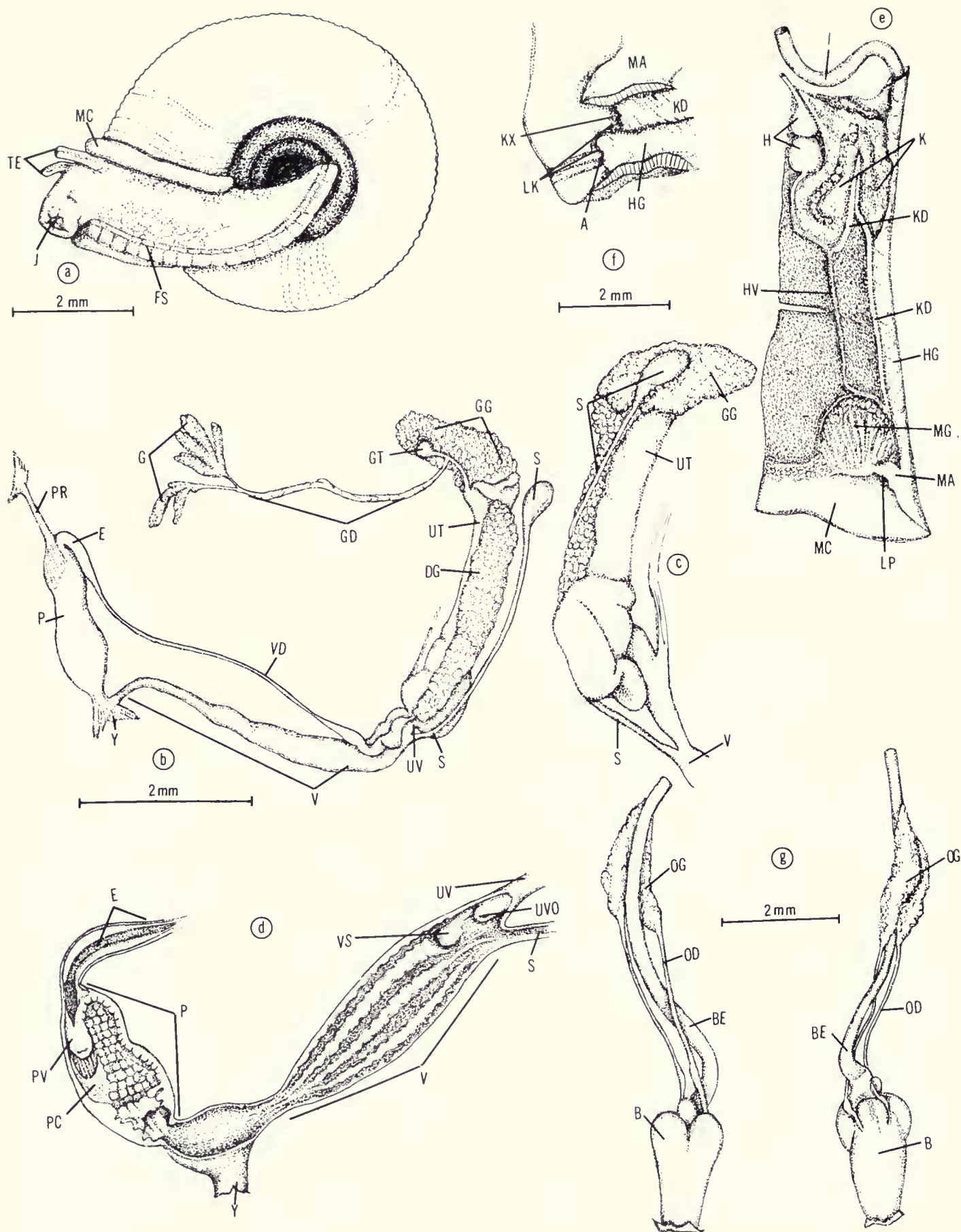


FIG. 9. Anatomy of *Charopa coma* (Gray). Waiwera-Puhi Road, north of Auckland, North Island, New Zealand. A. Solem! II-10-1962. FMNH 135420: a, left side of foot showing size relation to shell; b, genitalia; c, details of pallial genitalia; d, internal structures of penis and lower female tract; e, pallial region; f, details of pneumostomal area; g, bottom and top views of anterior digestive system. Scale lines as marked. (PS).



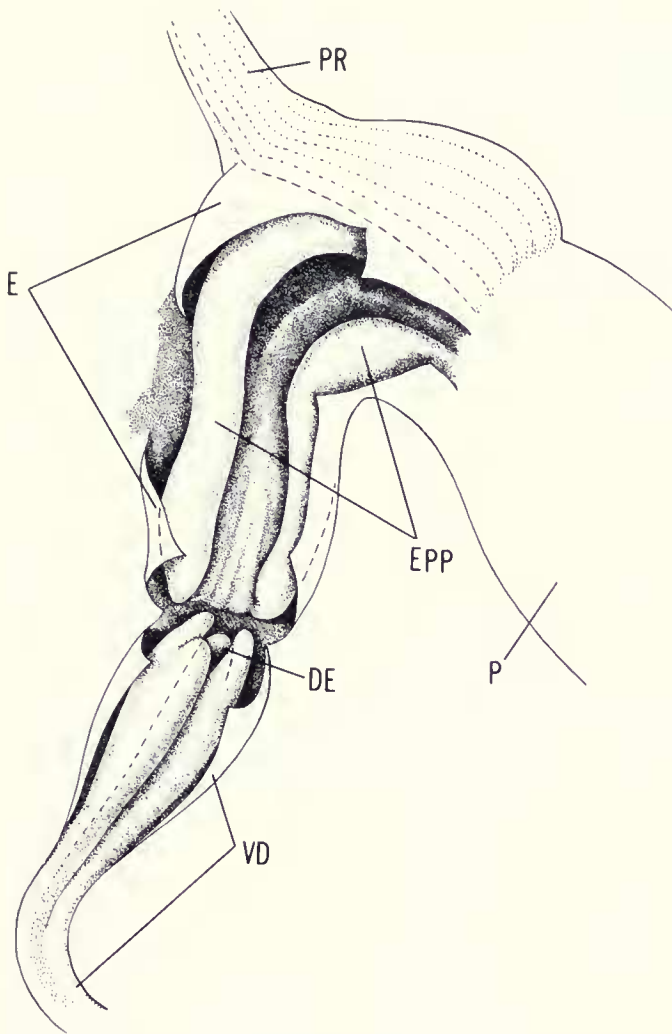


FIG. 10. Interior of lower vas deferens and epiphallus in *Charopa coma* (Gray). Waiwera-Puhoi Road, north of Auckland, North Island, New Zealand. A. Solem! II-10-1962. FMNH 135420. Greatly enlarged. (NB).

penis retractor muscle (PR) inserts as a U-shaped fan around the lower part of the epiphallus (E). Various modifications occur extralimitally in such taxa as *Phenacohelix pilula* (Reeve, 1852) (fig. 11). Here the penial retractor muscle inserts on the head of the epiphallus, and the vas deferens enters almost laterally. The shift in muscle attachment is relatively insignificant, but does make external recognition of the epiphallus presence difficult if not actually impossible.

The Pacific Island Charopinae mostly show, insofar as it could be checked, a specialized vas deferens-epiphallus junction (figs. 57e, 79c). Exceptions are found in *Graeffedon* and the provisionally assigned *Discocharopa* (see below). A circular sphincter surrounds the epiphallus pore (DE), and a Y-shaped plug extends through the pore to attach onto the wall of the epiphallus as a circular ridge. In general, the walls of the epiphallus are without sculpture or have the typical ridges (fig. 87c) seen in *Charopa coma* (Gray, 1843) (fig. 10). Because of size and preservation problems,

only a few of the species could be checked for this structure, and illustrations are given only for *Sinployea complementaria* (Mousson, 1865) (fig. 57e) and *Tuimalila pilsbryi* (fig. 79c). It was observed in several other *Sinployea*. Normally the head of the epiphallus expands abruptly, indeed it can be bulbous (fig. 67a), so that external recognition is easy.

In the Semperdoninae (figs. 100b, e-g, 102a, 103a, c-d), the vas deferens remains a thin tube during its ascent and enters laterally into the epiphallus, with the penial retractor muscle inserting directly onto the head of the epiphallus. The exact point of entry of the vas deferens into the epiphallus differs. In *Himeroconcha* and *Ladronellum* the entry occurs slightly below the rounded head (fig. 102d), whereas in *Semperdon* the entry is right next to one edge of the penial retractor muscle insertion (fig. 100i). The epiphallus is a double-walled tube, sometimes coiled within the muscle sheath. The outer wall is a thin muscle sheath, and the inner a thick glandular tube usually rolled inward on one side.

In the Trukcharopinae (figs. 90b-d, f-g, i-j, 93b-c, f, h) the vas deferens enters directly into the penis through a simple pore. In all examined genera except *Jokajdon* (fig. 93b-c) the vas deferens passes through the muscle fan before entering the penis. In *Jokajdon* the muscle insertion is directly on the head of the penis, and the vas deferens enters lateral to the insertion. This is interpreted as a secondary modification probably resulting from reduction in size. The Trukcharopinae thus have no trace of an epiphallus.

In the Rotadiscinae (H. B. Baker, 1927, pl. 16, fig. 14; pl. 17, figs. 22, 27) the epiphallus is less clearly differentiated externally, and it is either before (*Radioconus*) or after (*Rotadiscus*, *Radiodiscus*) insertion of the penial retractor muscle. The enlarged pilasters of the epiphallus are the main differentiating features.

In all of the Pacific Island Charopidae examined to date the penial retractor muscle originates from the diaphragm near the apex of the pallial cavity and inserts onto the penis or epiphallus. There is no shift to the columellar muscle equivalent to that seen in the Endodontidae (Solem, 1976b, pp. 81-83), which permitted elongation of the penis in such taxa as *Endodonta* and *Australdonta*. In addition, generally the penial retractor muscle in the Charopidae is very short, at times scarcely a tuft connecting the diaphragm and penis or epiphallus head. This is another correlative of the reduced whorl count in the Charopidae as compared with the Endodontidae.

With a few exceptions, the external appearance of the penis in the Pacific Island Charopidae is for a bulbous apical section that then tapers either abruptly or quickly to a slender stalk of variable length that joins the vagina to form the short atrium. The degree of the apical bulge depends directly upon the size and complexity of the internal pilasters and vergic structures. Figure 67 gives a fair sample of shape variations, and

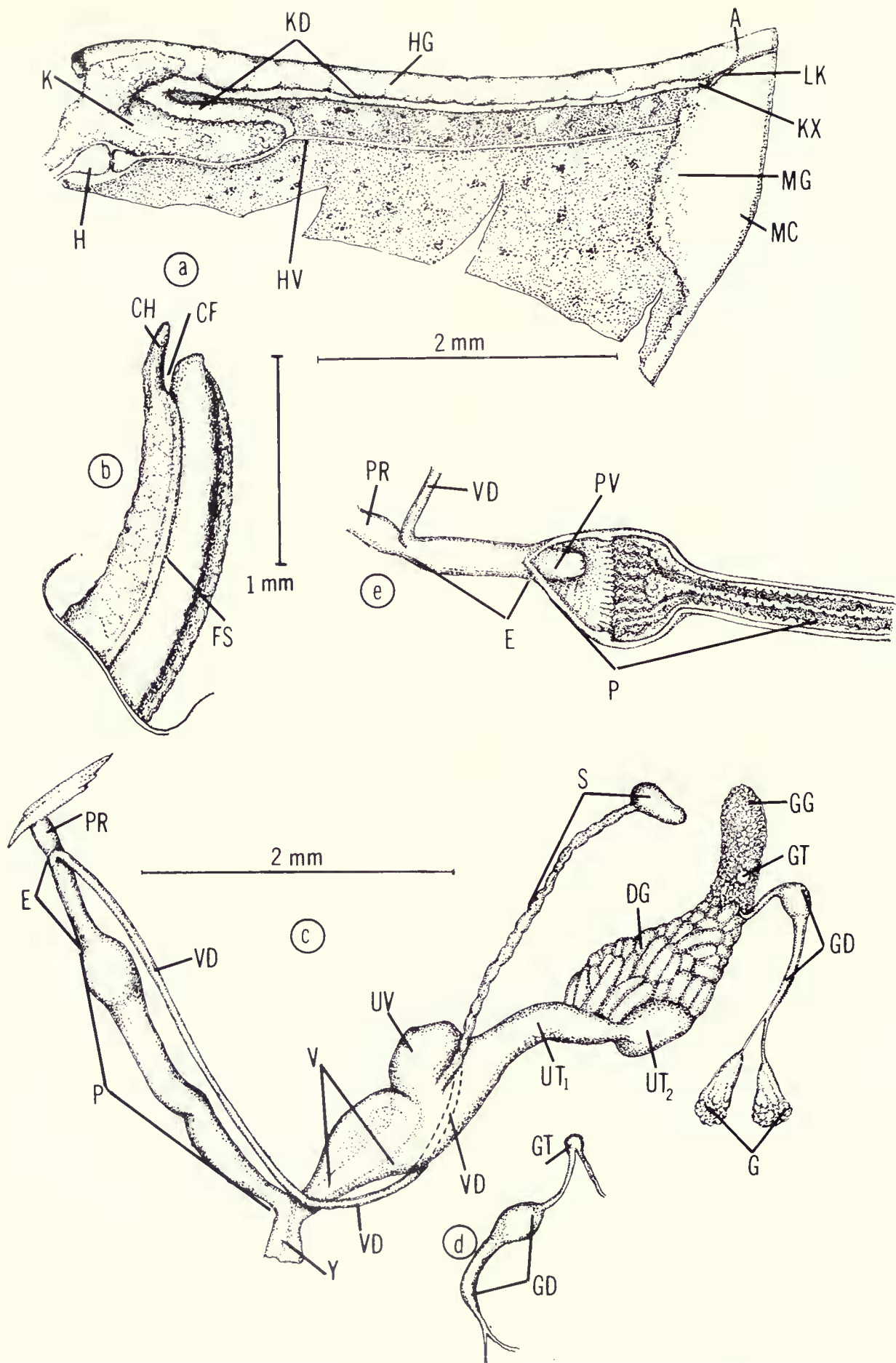


FIG. 11. Anatomy of *Phenacohelix pilula* (Reeve). Church Road, Kaitaia, Northland, North Island, New Zealand. L. Price! X-1962. FMNH 135421: a, pallial region; b, extended foot showing caudal horn (CH) and pedal grooves (FS); c, genitalia; d, junction of hermaphroditic duct (GD) and talon (GT); e, internal structure of penis. Scale lines as marked. (PS).



this is within a single genus. The major exception is the Semperdoninae (figs. 100, 102, 103) where a penis sheath, narrowed collar between epiphallus and penis, plus a quite different pattern of internal structure have combined to produce a more tubular appearance. It is not possible to assign a species to a genus on the basis of the external penis appearance. The internal structures must be examined. They differ radically from subfamily to subfamily, and within a genus are subject to extensive modifications for species recognition purposes. A review of structure on a subfamily by subfamily basis is required.

In the Charopinae from Australia, New Zealand, New Caledonia, Lord Howe Island, South Africa, St. Helena, and South America there is an amazing amount of variation that will have to be dealt with elsewhere. Comments here will be restricted to the type genus, *Charopa* Albers, 1860, *Phenacohelix* Suter, 1892, and the Pacific Island taxa. *Charopa coma* (Gray, 1843) has the penis with only a modestly swollen exterior (fig. 9b) and a very short basal stalk portion. Internally (fig. 9d) it shows an apical verge (PV) with near terminal slitlike pore, below this is a pocket stimulator (PC), followed by a series of variable-sized circular pilasters that occupy a quite low position. In addition, the upper and middle walls of the penis chamber have raised, soft pustules. *Phenacohelix pilula* (Reeve, 1852) has a much elongated and more slender penis (fig. 11c), with shifted position of the epiphallus (E) to below the insertion of penial retractor muscle (PR). Internally (fig. 11e) a small verge (PV) with terminal pore lies above a series of corrugated longitudinal pilasters and a vague swelling that I interpret as a remnant of the pocket stimulator. The verge and ridge correspond to the external bulge on the penis section. The sculpture of the wall, position and number of circular ridges, size of pocket stimulator, and verge size differ between *Phenacohelix* and *Charopa*, but the fact of a basic set of structures is the important data.

In most of the Pacific Island Charopinae there is simple variation in the relative sizes of the verge, pocket or modified pocket stimulator, and the number and prominence of the circular bands. The wall sculpture found in the New Zealand taxa seems to be absent in the Pacific Island taxa. The combination of very small size (see table XV), limited material, and preparation of illustrations at an early stage in the study means that treatment of the variations in this portion of the study is inadequate. Specific comments on differences between geographically close species are given in appropriate places in the systematic review. Here I will mention only a few more obvious changes. The verge varies from a small spade-shaped papilla with open side (fig. 42e, *S. peasei*), to a conical projection with terminal pore (fig. 43e, *S. avanaensis*), or it is reduced to a swelling attached to one wall (fig. 55e, *S. allecta*), or a globular swelling (fig. 57c, *S. complementaria*, fig. 75h, *Ba humbugi*), a protruding lobe with laterally apical pore (fig. 79c, *Tuimalila pilsbryi*),

or the bulbous structure seen in *Vatusila tongensis* (fig. 84b).

The circular ridge can be split into several and low (fig. 42d–e, *Sinployea peasei*), doubled and thick (fig. 43e, *S. avanaensis*), single and thin (figs. 51h, *S. intermedia*; 57c, *S. complementaria*; 67j, *S. euryomphala*), or very thick and partly altered into pads (figs. 55e, *S. allecta*, 79c, *Tuimalila pilsbryi*).

The pocket stimulator is particularly variable and with few exceptions has been inadequately illustrated and interpreted. Comparison of the doughnut shape in Figure 39h, split "U" in Figure 42d, raised globular mass in Figure 53c, low "U" in Figure 53h, lobular structure in Figure 55e, "U" ridge in Figure 67d, widely open pocket in Figure 67j, greatly reduced and altered structure in Figure 75h, and nearly closed pocket in Figure 79d gives an idea of the great extent of variation in this structure, but this is only an introduction to its complexity.

This study demonstrates that extensive variation occurs in verge, circular ridges, and pocket stimulator in the Pacific Island Charopinae, but analysis of the patterns of variation is beyond the scope of this report. Because *Sinployea* is evidently in a highly active stage of speciation, study of this area might yield important data, but is left for others.

A major modification of this pattern occurs in *Graeffedon* (fig. 87c). The epiphallus (E) opens through a simple pore that is surrounded by a huge circular pilaster (PP). Immediately below this are three large pilasters: an upper, free-tipped vergic stimulator, a long and low semicircular ridge oriented longitudinally in the penis chamber, and a broad, low ridge with slightly free upper tip that occupies the lower half of the penis. Coupled with the absence of the valve at the vas deferens-epiphallus junction, these structures mark *Graeffedon* as remote from the other Charopinae, but it is better accommodated in this subfamily than assigned to one of its own.

The Trukcharopinae (fig. 90c–d, g, i) have a simple pore opening from the epiphallus (*Russatus*), a low vergic papilla (*Kubaryiellus*), or even a tubular verge (*Palline*). Various pilasters and a possibly highly modified pocket stimulator are found in some of the taxa. These variations are discussed more fully on pp. 205–207. Many of these represent additive structures compared with the Charopinae, but basically they could be derived from some of the Charopinae conditions in extralimital taxa (Solem, unpublished data).

The Semperdoninae (figs. 100d, f, j, 102d, 103b, f) have the epiphallus entering the penis through a narrow muscular collar, with high lamellar pilasters extending down and then usually coalescing into three, high glandular pilasters. The whole penis is surrounded by a muscular sheath. Exceptions to the basic pilaster pattern are *Himeroconcha rotula* (Quadras & Möllendorff, 1894), which lacks the initial radiating pilasters although retaining the three basal ones, and *Ladronellum mariannarum* (Quadras & Möllendorff,

1894) in which the initial radiating pilasters coalesce into a huge horseshoe-shaped pilaster (fig. 102d) that is inflatable with fluids. The enclosure of both epiphallus and penis by a muscle sheath is as great a change as is the pilaster pattern. These make the Semperdoninae the most isolated of the charopid subfamilies in terms of penis structure.

In the few dissected Rotadiscinae (H. B. Baker, 1927; Solem, unpublished data) the epiphallus enters through a pore, papilla, or short verge into a very thick-walled chamber with longitudinal pilasters. There may or may not be accessory organs associated with the penis and/or atrium. This represents yet another series of experiments in the Charopidae.

Finally, the situation in *Discocharopa* (fig. 34c) requires comment. A short, tubular penis with lateral entrance of the vas deferens has the penial retractor muscle inserting apically. Apparently there are at least two longitudinal pilasters inside the penis, but the available material was not adequate to work out the details (see p. 75). Although this departs from the reported pattern for the Charopinae (see above), the genus is temporarily placed in the Charopinae pending revision of the extralimital groups. It probably will be split into another subfamily unit, but available data are inadequate to propose a more appropriate classification.

The atrium, in all dissected material, is a simple, short tube opening externally behind and above the right rhinophore. It varies somewhat in length but shows no really significant changes.

**TERMINAL FEMALE GENITALIA**—The post-uterine or free oviduct (UV), spermatheca (S), and vagina (V) in the Endodontidae are very slender tubes without unusual structures. They show variation primarily where the spermathecal shaft inserts—penis, atrium, or free oviduct (Solem, 1976b, pp. 83–84). In the Charopidae the situation is quite different. Normally, the spermathecal base and at least parts of the vagina are greatly enlarged and with complex internal pilasters. The free oviduct, most of the vagina, and the spermathecal shaft above the swelling will be quite slender, with an ovate, expanded head of the spermatheca buried in the albumen gland-prostate margin. The shape and proportions shown by *Sinployea avanensis* (fig. 43c) are typical. The shifted expanded area in *S. aunuuana* (fig. 53b) or expanded free oviduct (UV) in *S. allecta* (Cox, 1870) (fig. 55c), shortened vagina in *S. inermis lakembana* (fig. 67f), and generally greater elongation in the Semperdoninae (figs. 100b, e, g, 102a, 103a, c–d) are the typical minor variations. The nearest thing to a major variation is found in *Jokajdon* (fig. 93b–c) where the expanded area is restricted to the base of the vagina and atrium, and the normally expanded areas are slender in comparison. In addition there is an accessory muscle attaching to the penioviducal angle. These changes may correlate with the very restricted shell aperture and large barriers of *Jokajdon*.

Internally there appear to be two basic patterns of sculpture of the upper vagina and lower spermatheca. In the typical Charopinae, such as *S. complementaria* (Mousson, 1865) (fig. 57f), *S. allecta* (Cox, 1870), and *Ba humbugi*, there are weak longitudinal pilasters in the vagina, the free oviduct (UV) has a constricting pilaster with central pore (UVO), and the opening of the spermatheca (S) has a central pore (SO) through a circular pilaster with one edge a free flap. Because of size problems and the early stage in the study at which this area was examined, only the one has been illustrated. The second pattern is seen quite clearly in *Graeffedon* (fig. 87c) where the opening to the free oviduct is a simple pore and there are huge longitudinal pilasters lining the walls of the spermatheca and vagina. Essentially the same pattern is seen in *Palikirus*, *Palline*, *Semperdon uncatatus*, *S. heptaptychius* (Quadras & Möllendorff, 1894), *Ladronellum mariannarum* (Quadras & Möllendorff, 1894), *Himeroconcha lamlanensis*, and *H. fusca* (Quadras & Möllendorff, 1894), thus indicating that this general type occurs not only in some of the Charopinae, but also in the Trukcharopinae and Semperdoninae. A detailed comparative study of this region would be well worthwhile but is beyond the scope of this monograph.

#### PALLIAL COMPLEX

A discussion of the functional significance that the closed and complete ureter found in most Charopidae has in relation to water conservation as contrasted to the incomplete posteriorly opening ureter of the Endodontidae was given previously (Solem, 1976b, pp. 84–87). Some of the New World Rotadiscinae show only a partial closed ureter (H. B. Baker, 1927, pl. 16, fig. 17, pl. 17, figs. 24, 30), and there are Australian equivalents (Solem, unpublished data). All of the Pacific Island Charopidae that have been dissected show a complete ureter with the ureteric pore opening next to the anus just inside the pneumostome. This contrasts immediately with the Endodontidae where the ureteric pore opens at the posterior part of the pallial cavity near where the anterior margin of the rectal kidney lobe touches the hindgut (Solem, 1976b, p. 85, fig. 49c). Thus, even a glance at the anterior part of the pallial cavity is sufficient to tell whether a Pacific Island species belongs to the Endodontidae or Charopidae.

A typical charopid configuration is seen in *Sinployea allecta allecta* (Cox, 1870). Viewed from the outside (fig. 55a), the bilobed nature of the kidney (K) is obvious, with the longer, cigar-shaped rectal lobe (lower in figure) definitely overlapping the hindgut (HG). The shorter, irregularly shaped pericardial lobe (upper in figure) partly overlies and is cupped partly around the heart (H). The kidney base (left in figure) stops short of the downward twist of the hindgut as intestine and is abutted by the lobules of the digestive gland. The primary ureter (KD) originates from near the anterior margin of the pericardial lobe of the kid-



ney, follows the upper margin of this lobe posteriorly, lying partly on the pallial cavity roof and partly on the kidney itself, reflexes abruptly and as the secondary ureter follows the lower margin of the rectal kidney lobe anteriorly to its termination, then lies next to the hindgut until both disappear under the mantle collar (MC). The principal pulmonary vein (HV) extends anteriorly from the heart along the pallial roof, but in the smaller species shows no sign of branching, fading out from visual observation well short of the mantle collar.

The bilobed kidney, or in a torn and extracted specimen, the tip of the rectal lobe of the kidney, plus the presence of the secondary ureter as a distinct tube next to the hindgut, are sufficient to immediately identify a species as a member of the Charopidae or Punctidae rather than the Endodontidae. In the latter family (Solem, 1976b, p. 459, fig. 195a) there is at most a short rectal lobe with the ureter ending in a ureteric pore (KX) as it reaches the hindgut. In a few Charopidae, such as *Phenacohelix pilula* (Reeve, 1852) (fig. 11a), the rectal arm is as short as in the Endodontidae, but the clear presence of the secondary ureter along the hindgut is sufficient for family separation. Exceptions to this in some Australian taxa will be considered elsewhere.

When dissected out (fig. 55b) and viewed from an inside view of the pallial cavity, the typical charopid pallial region shows only minor additional features. Remnants of a retractor muscle to a rather strongly developed muscle come off the parietal-palatal margin near the kidney base. A weaker version of the same muscle can be seen in many species of Endodontidae (Solem, 1976b, p. 459, fig. 195a). The heart in this view clearly lies on top of the kidney, the rectal kidney lobe extends partly under the hindgut, thus overlapping on both sides of this tube, and both the hindgut and ureter terminate just inside the mantle collar. Quite possibly this area is involved in water resorption and is a precursor of the more elaborate structures seen in higher aulacopods, such as an apparent bladder in *Deroceas reticulatum* (Müller, 1774) (Runham & Hunter, 1970, pp. 77–79, figs. 32–33).

Modifications of this general pattern involve addition of new structures, changes in the relative size of the kidney lobes, differences in the amount of space between the two lobes, and compactional alterations correlated with reduction in whorl counts. Data on at least part of the pallial complex was recorded for 36 of the 43 taxa for which at least some anatomical material was available. Illustrations are presented for 20 of these. The only additive structure seen in a Pacific Island taxon is the extensive intrusion of mantle gland tissue onto the pallial roof in *Graeffedon graeffei* (Mousson, 1869) (fig. 87a, MG) and a slight extension in *Semperdon xyleborus*. This phenomenon is far more common in extralimital taxa, with the intrusion ranging from a massive and sharply defined area in *Charopa coma* (Gray, 1843) (fig. 9a) to the short area in *Phenacohelix pilula* (Reeve, 1852) (fig. 11a) and the

elongated finger in *Laoma leimonias* (Gray, 1850) (fig. 25a). The function of this extension is unknown.

Although there is a modest amount of intraspecific variation in the relative length of the two kidney lobes, much of this seems to be caused by differential contraction and compaction when the animal withdraws into the shell. Dissections made from deeply retracted specimens tended to have the rectal kidney lobe unchanged in shape and position, but pulled back further relative to the heart and pericardial kidney lobe. The latter would tend to be somewhat twisted and distorted (for example see fig. 34d). I made no exact measurements as to the relative lengths because the results would not be strictly comparable. Table IX summarizes the relative lengths in the Pacific Island species. Only in *Discocharopa aperta* (Möllendorff, 1888) (fig. 34d) is the rectal lobe somewhat reduced to as great an extent as in the New Zealand *Phenacohelix pilula* (Reeve, 1852) (fig. 11a). The general pattern is for the rectal lobe of the kidney to be much longer than the pericardial. This reaches its greatest extent in such taxa as *Graeffedon graeffei* (Mousson, 1869) (fig. 87a) and *Semperdon heptapychius* (Quadrass & Möllendorff, 1894) (fig. 100a). In both of these taxa the pericardial lobe is reduced to a small fraction of the length and volume of the rectal.

The length relationship varies within a genus, since in *Sinployea* there are nine species in which the

TABLE IX. — RELATIVE LENGTH OF KIDNEY LOBES  
IN THE PACIFIC ISLAND CHAROPIDAE.

Subequal or Equal	Rectal Much Longer	Pericardial Much Longer
<i>Sinployea tahitiensis</i>	<i>Sinployea modicella</i>	<i>Discocharopa aperta</i>
<i>S. lamellicosta</i>	<i>S. montana</i>	
<i>S. avanaensis</i>	<i>S. neglecta</i>	
<i>S. intermedia</i>	<i>S. peasei</i>	
<i>S. allecta allecta</i>	<i>S. aunuuana</i>	
<i>S. vicaria vicaria</i>	<i>S. clista</i>	
<i>S. kusaieana</i>	<i>S. complementaria</i>	
<i>S. inermis inermis</i>	<i>S. irregularis</i>	
<i>S. i. lakemba</i>	<i>S. euryomphala</i>	
<i>S. adposita</i>	<i>Graeffedon graeffei</i>	
<i>Ba humbugi</i>	<i>Kubaryellus kubaryi</i>	
<i>Tuimalila pilsbryi</i>	<i>Trukcharopa trukana</i>	
<i>Russatus nigrescens</i>	<i>Palikirus cosmetus</i>	
<i>Himeroconcha fusca</i>	<i>Jokajdon callizonus</i>	
<i>H. lamlanensis</i>	<i>Palline notera notera</i>	
	<i>P. micramyla</i>	
	<i>Semperdon uncatus</i>	
	<i>S. xyleborus</i>	
	<i>S. heptapychius</i>	
	<i>S. rotanus</i>	
	<i>Ladronellum mariannarum</i>	

kidney lobes are equal or nearly equal in length and nine in which the rectal is significantly longer. I could detect no conchological correlations in size, shape, or whorl count with this variation in kidney lobe length concerning *Sinployea*. The other Charopinae have a secondarily shortened and very fat kidney correlated with whorl count reduction (*Ba humbugi*, fig. 75a), subequal lobes in the gigantic *Tuimalila pilsbryi* (fig. 79a), or the very elongated rectal lobe in *Graeffedon graeffei* (Mousson, 1869) (fig. 87a). In the Trukcharopinae only *Russatus nigrescens* (Möllendorff, 1900) (fig. 90a), whose whorl count is reduced to a mean of  $3\frac{1}{2}+$ , has a shortened kidney, whereas in the Semperdoninae only the large-sized *Himeroconcha* have the kidney lobes equal or subequal in length.

In both the Trukcharopinae and the Semperdoninae the arms of the ureter are tightly pressed together without any pallial roof tissue visible between them. The pattern is somewhat unusual in *Russatus nigrescens* (Möllendorff, 1900) (fig. 90a), with the abrupt angling of both ureter arms at the anterior margins of the kidney lobes. I interpret this as the result of shortening and secondary thickening of the kidney in relation to whorl and pallial cavity reduction. In the Charopinae, the same compaction is seen in *Ba humbugi* (fig. 75a), with only slightly less abrupt and extensive angling of the ureter. Of the examined *Sinployea*, all taxa except *S. allecta allecta* (Cox, 1870) (fig. 55a–b) and *S. irregularis* (Garrett, 1887) have at least a narrow strip of pallial roof tissue visible between the ureter arms, as does *Tuimalila pilsbryi* (fig. 79a). Extralimital Charopinae are variable in this feature (see figs. 9e, 11a).

Shortening of the pallial cavity is more common than elongation. The latter seems to have occurred only in *Jokajdon callizonus* (Möllendorff, 1900) (fig. 93a) where it extends  $\frac{3}{4}$  of a whorl apically. This probably correlates with the narrowed cross-section of the body whorl in this species (fig. 92b). Major shortening has occurred in *Ba humbugi* (fig. 75a) and *Russatus nigrescens* (Möllendorff, 1900) (fig. 90a). Their respective mean whorl counts of  $3\frac{3}{8}$  and  $3\frac{1}{2}+$  are the lowest in the Pacific Island Charopidae, except for the rotadiscine *Microcharopa mimula* (mean whorl count  $3\frac{1}{4}-$ ). In both *Ba* and *Russatus* the width of the kidney is almost equal to its length, and the arms of the ureter are tightly compacted and overlap each other between the kidney lobes. The process has been carried further in *Russatus*, with  $\frac{1}{4}$  whorl length to the pallial cavity, than in *Ba*, where the length is still  $\frac{1}{2}$  whorl. The same type of compaction has occurred in both genera, and they form a contrast to the situation in the New Guinea charopids *Pilsbrycharopa* and *Paryphantopsis* (Solem, 1970a, p. 250, fig. 2a, f) in which kidney compaction resulted in progressive increase of the angle between the arms of the ureter, and the kidney is rotated away from the hindgut. Yet another pattern is seen in the New Zealand flammulinid and *Maori-concha* groups.

The pallial cavities in the Pacific Island Endodon-

tidae and Charopidae have radically different ureter and kidney structures. Within the Pacific Island Charopidae there is a relatively simple pattern of variation in relative lengths of the kidney lobes and the extent to which lung roof tissue is visible between the arms of the ureter.

#### DIGESTIVE SYSTEM

Allowing for the generally reduced whorl counts (table X) in the Charopidae, the gross features of the endodontid (Solem 1976b, pp. 372–373, figs. 163–164) and charopid (figs. 9e, g, 75a) digestive tracts are the same. The digestive glands (OG) are in contact above the esophagus (BE), which continues past the pallial cavity as a slender tube. In some taxa, such as the larger *Sinployea*, *Ladronellum mariannarum* (Möllendorff, 1900), and *Kubaryellus kubaryi* (Möllendorff, 1900), the salivary glands are fused above the esophagus, whereas in *Ba humbugi*, they do not even touch posteriorly. I am not certain if there is any systematic significance to these changes. Intestinal loops above the pallial cavity apex occupy about  $\frac{1}{16}$  of a whorl, instead of the  $\frac{1}{8}$  whorl in the Endodontidae. The charopid stomach expansion averages about  $\frac{3}{4}$  of a whorl, with the digestive gland shorter and more compact than in the Endodontidae. Except for these changes associated with the reduced whorl count, the gross features of the digestive tract are the same in the two families.

Radular features are one of the best guides to separating the Endodontidae, Charopidae, and Punctidae on the Pacific Islands. The endodontid radula (Solem, 1976b, pp. 88–94, figs. 51–54) has a tricuspid central, several bicuspid laterals, and marginals that have the ectocone fragmented and the endocone increasing almost to the size of the mesocone. There are very noticeable differences in the angling of the individual teeth, but their small size and difficulties in mounting and preparation have prevented full study of their variation.

The punctid radula (fig. 12) presents a number of unusual features. The central tooth (fig. 12a, upper) has a long slender mesocone and two very slender, much shorter ectocones. The laterals (fig. 12b–e) have two slender cusps and three much shorter accessory cusps, whereas the outermost lateromarginals (fig. 12f) are broader and with the outer large cusp reduced in size. The accessory cusps are at to below the limit of optical microscope examination, depending upon the quality of the equipment and illumination. As far as I am aware, the only optical microscopist to detect and illustrate these accessory cusps was H. B. Baker (1927, pl. 16, fig. 11), also reprinted in Pilsbry (1948, p. 642, fig. 349, d).

In addition to the obvious cusp edges and numbers there are fundamental differences in the nature of the cusps and basal plates in the two families. The endodontid basal plate (Solem, 1976b, p. 89, fig. 52d) has a typical interlocking relationship with the next pos-



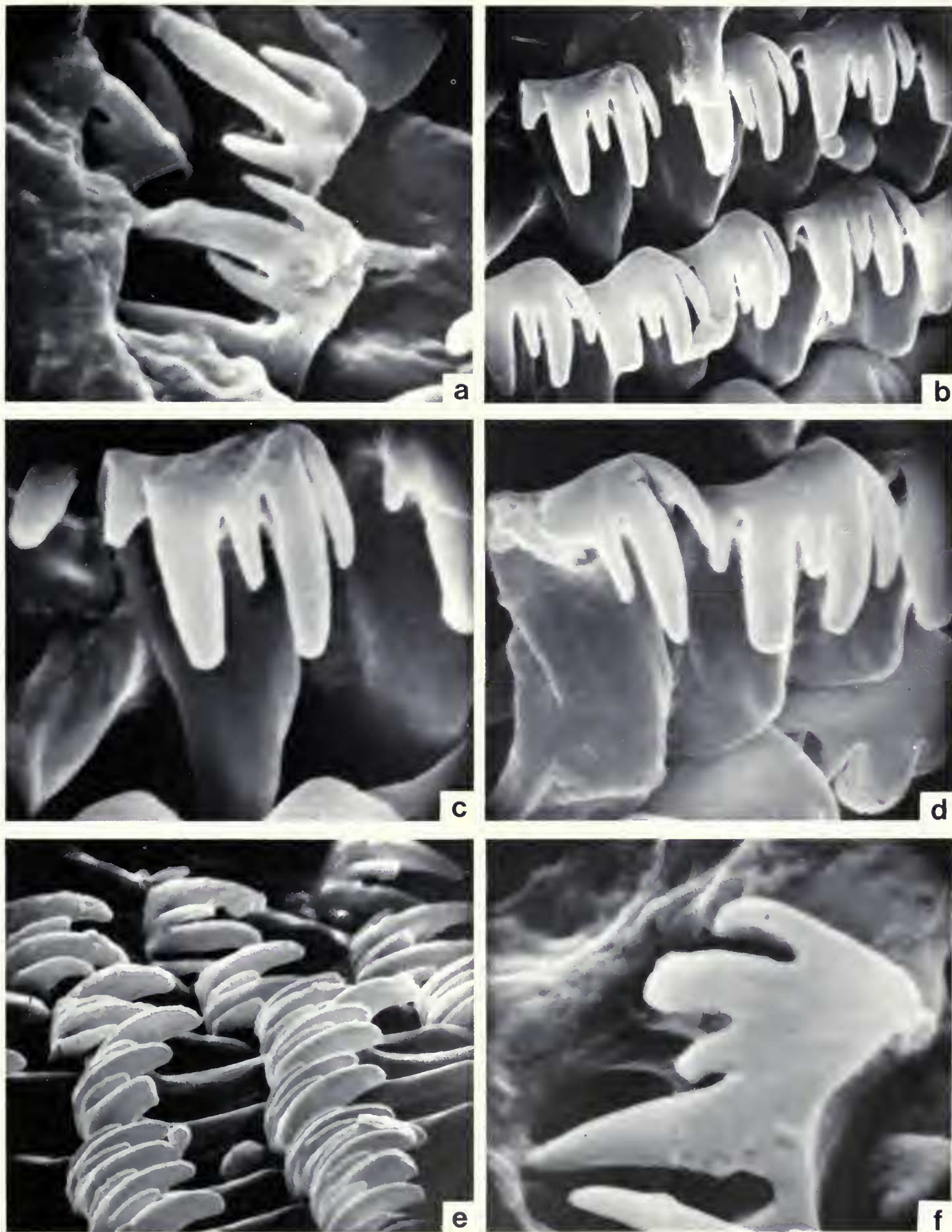


FIG. 12. Radular teeth of *Punctum minutissimum* (Lea). Cedar bog, Woodburn Road, 4 miles southwest of Urbana, Champaign County, Ohio. E. Kefer!! X-20-1969. FMNH 151102: a, central (upper) and 1st lateral (23,000 $\times$ ); b, early lateral teeth (10,800 $\times$ ); c, single midlateral tooth (21,500 $\times$ ); d, late lateromarginal teeth (15,900 $\times$ ); e, low angle view of lateromarginal teeth (10,700 $\times$ ); f, outer lateromarginal tooth showing cusp reduction (28,000 $\times$ ).

terior tooth, is square to rectangular in shape (Solem, 1976b, p. 91, fig. 54b, e), and, at least for the early lateral teeth, the cusps are sharply pointed and elevated at a high angle (Solem, 1976b, p. 88, fig. 51a–b; p. 89, fig., 52a–b, d). In the Punctidae (fig. 12c, e) the basal plate is long and tapering, has no apparent interlocking relationships, and the cusps are bluntly rounded and point almost directly forward. It is unfortunate that these differences can be seen only with the scanning electron microscope, a fact that reduces their routine utility in identification and classification.

The Pacific Island Charopidae have a very standard pattern of structure (figs. 13–14). As pointed out earlier (Solem, 1976b, p. 93), extralimital charopids show a variety of structure, but review of these is outside the scope of this monograph. The tricuspid central tooth (figs. 13b, 14a) is slightly narrower and shorter than the adjacent laterals, which are tricuspid. When viewed at a low angle, it is evident that the side cusps of both central and laterals are raised above the elevation plane of the mesocone (fig. 14a), whereas in the Endodontidae (Solem, 1976b, p. 88, fig. 51a) they are in the same elevation plane. The outer laterals and early marginals in the Charopidae (fig. 14b) do not have the elevated side cusps. The marginals may retain the tricuspid pattern (fig. 13c–f), or rarely the outer marginals may become multicuspid. Climo (1969a, figs. 31–34; 1970, figs. 11–14) gives a number of radular transects for New Zealand charopids.

Because only a few species could be examined with the SEM and their pattern of structure was quite uniform, results from optical viewing mostly have been omitted from the text in this volume.

The bicuspid laterals of the Endodontidae, tricuspid laterals of the Charopidae, and multicuspid lateromarginals of the Punctidae found on Pacific Islands thus present clearcut differences among the families. The Austro-Zelandic charopids, however, show a great variety of radular structures, so that the endodontid-charopid distinction does not hold for that area.

Jaw structure in the Charopidae was not studied in detail because the pattern of partial plate fusion in larger taxa paralleled the situation found in the Endodontidae (Solem, 1976b, p. 94).

#### FREE MUSCLE SYSTEM

As in the Endodontidae (Solem, 1976b, p. 94), all dissected charopids had the right ommatophoral retractor passing through the penioviducal angle and joining the right rhinophoral retractor that passes outside the penioviducal angle posteriorly. Unlike the Endodontidae, in all examined Charopidae the penial retractor muscle arises from the diaphragm and inserts onto the penis or epiphallus. Only a few alterations in the common pattern of unions were observed. *Russatus nigrescens* (Möllendorff, 1900) has the tentacular retractors fusing with the tail fan at the columellar muscle rather than earlier as in most taxa. In *Jokajdon*

*callizonus* (Möllendorff, 1900) a new muscle attaches at the penioviducal angle, joining the tail fan much later. With the elongated ( $\frac{3}{4}$  whorl) pallial cavity and narrowed aperture with large barriers (fig. 92b) in this species, the added muscle may play a major role in successful body retraction.

In *Sinployea complementaria* (Mousson, 1865) there is a muscle from the right tentacular retractor that inserts on the apex of the free oviduct, whereas in *Tuimalila pilsbryi* a muscle runs from the columellar retractor to the apex of the free oviduct. It is possible that a weaker version of this same muscle is present in smaller species of Pacific Island Charopidae and was overlooked in earlier phases of this study. It was not possible to recheck all taxa for this feature. Extralimital taxa, such as *Stephanoda binneyana* (Pfeiffer, 1847) (fig. 31c), show a vaginal retractor muscle (VRM). It is probable that a number of such experiments in added muscles exist, but have not been observed.

#### NERVOUS SYSTEM

Wherever possible, the enervation of the penis from the right cerebral ganglion was confirmed, but because of difficulties in handling the small-sized material, preservation in alcohol, and heavy covering of connective tissue over the ganglia, no attempt at working out the details of the nervous system was made. Climo (1970, fig. 21B) illustrated the central nervous system of *Phenacharopa novoseelandica* (Pfeiffer, 1853).

#### EXTERNAL BODY FEATURES

In the Trukcharopinae and Semperdoninae, except for *Semperdon heptapychius* (Quadrass & Möllendorff, 1894), *Ladronellum mariannarum* (Quadrass & Möllendorff, 1894), and *Himeroconcha fusca* (Quadrass & Möllendorff, 1894), the body color is yellow-white, without darker markings. In the latter three species there are gray to reddish gray markings on the neck, ommatophores, and mantle collar. In the Charopinae, all live-collected Cook, Society, and Samoan Island species of *Sinployea*, except the Swains Island *S. intermedia*, have light to dark gray markings. All of the *Sinployea* with gray markings have been taken in semiarboreal situations. The purely terrestrial *S. kusaieana*, *S. euryomphala*, *S. inermis*, *S. adposita*, and *S. irregularis* (Garrett, 1887) have yellow-white body color. *Tuimalila pilsbryi* also shows the darker mantle and neck coloration. The dark body color appears to be a correlative of semiarboreal habitat.

Many of the arboreal New Zealand and Australian charopid taxa have a strongly developed mucus apparatus at the hind end of the foot. A typical "mucus pore" or "caudal foss" (CF) is present in *Phenacohelix pilula* (Reeve, 1852) (fig. 11b), with the pore overhung by a caudal horn (CH). This is effectively an intensification of the point where the foot grooves unite above the tail plus a mucus-secreting gland concentrating at



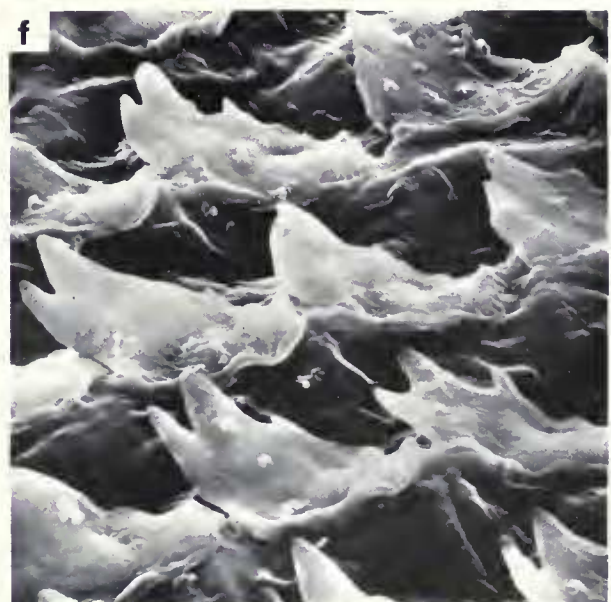
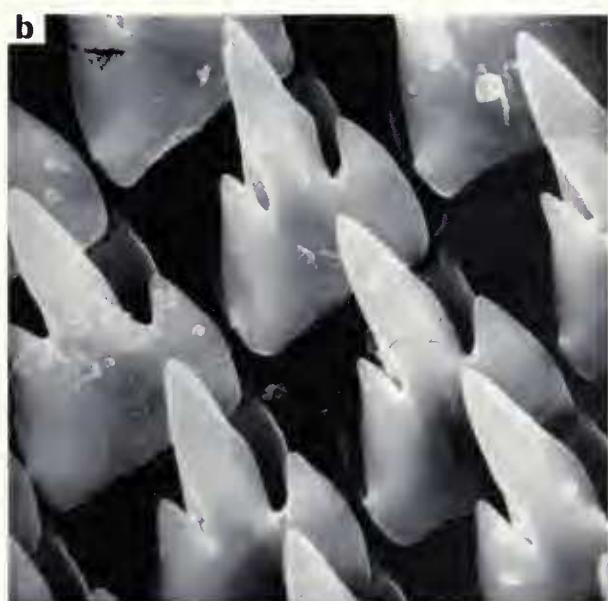
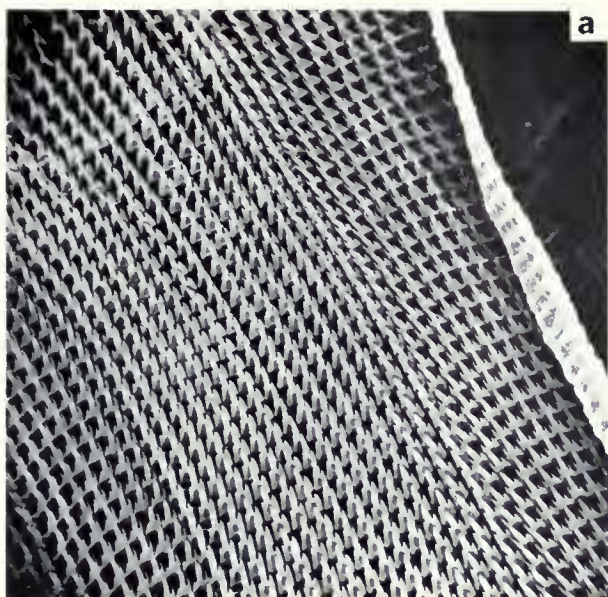


FIG. 13. Radular teeth of *Tuimalila pilsbryi*. Station T-22, 1,000 ft. elevation, Eua, Tonga. FMNH 152378: a, near middle of radula at 280 $\times$ ; b, central tooth and 1st lateral on right side of radula at 2,820 $\times$ ; c, early laterals on right side of radula at 2,900 $\times$ ; d, transition from laterals to marginals on left side of radula at 2,950 $\times$ ; e, middle marginals from left side at 2,875 $\times$ ; f, outermost marginals at 2,875 $\times$ . All views nearly vertical.



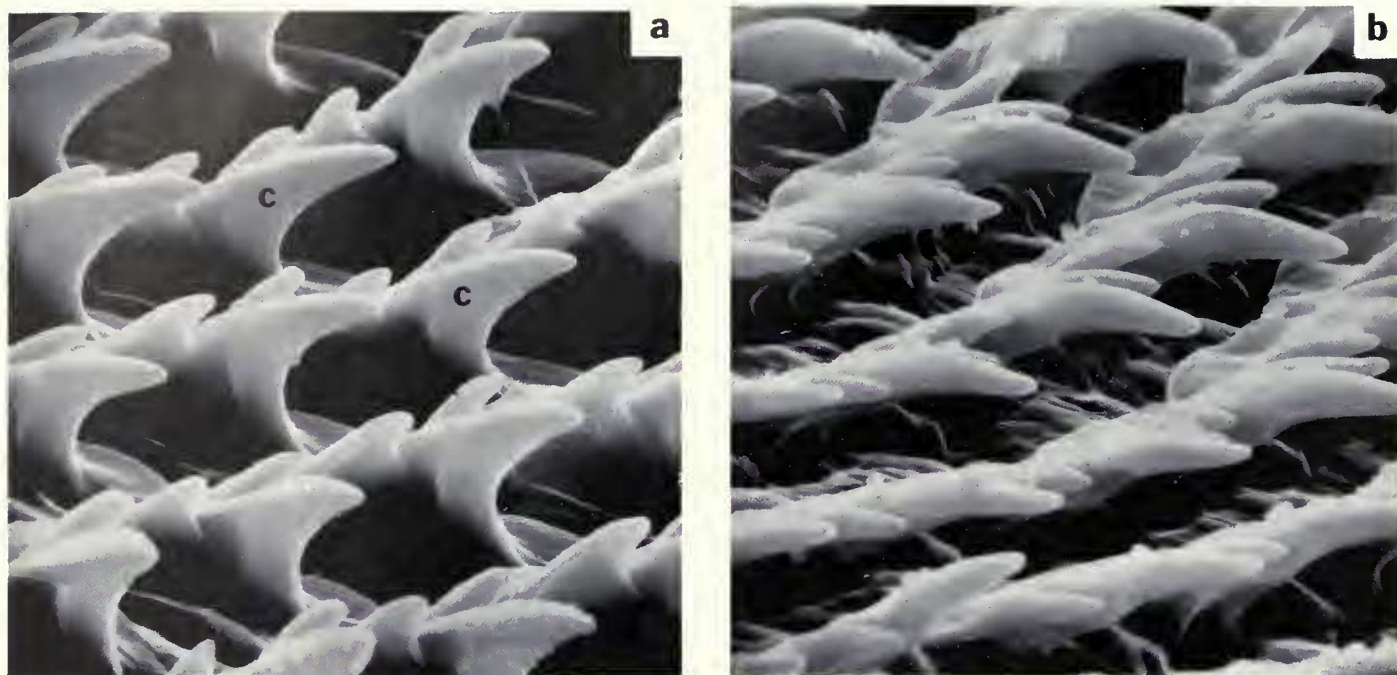


FIG. 14. Radular teeth of *Tuimalila pilsbryi*. Station T-22, 1,000 ft. elevation, Eua, Tonga. FMNH 152378: a, 45° angle view of central (c) and early laterals at 3,200 $\times$  showing pattern of cusp elevation; b, same view of transitional zone between laterals and marginals at 3,125 $\times$ .

this point. This apparatus is absent in *Charopa coma* (Gray, 1843) (fig. 9a) and all of the dissected Pacific Island Charopidae (fig. 43a). The presence of this pore is associated with arboreal snails (Solem, 1976b, pp. 105–106) and is not of major phyletic importance, as was also confirmed by Pilsbry (1892a–b, 1893a–b) and Climo (1969a, pp. 148–150).

As in the Endodontidae (Solem, 1976b, p. 94), the mantle collar normally is without protrusions, the gonopore is located below and slightly behind the right ommatophore, and the slime network is rather weakly defined. Neither family shows substantial external modifications in the Pacific Island taxa.

#### PATTERNS OF VISCERAL HUMP REDUCTION

In the Endodontidae (Solem, 1976b, pp. 94–98) one of the major repetitive changes is an increase in the number of whorls and thus elongation of the visceral hump. Not only do the Pacific Island Charopidae have a much lower average whorl count than the Endodontidae (median means  $4\frac{1}{8}$ – and  $5\frac{1}{2}$ +, respectively), but of the Charopidae only *Semperdon kororensis* (Beddome, 1889) with  $5\frac{1}{8}$  whorls and the Rarotongan *Sinployea planospira* (Garrett, 1881) with  $6\frac{5}{8}$  whorls exceed a mean count of five whorls. The latter has not been taken in this century, and of the former only fragmentary extracted pallial collars and terminal genitalia were available. Thus I can offer no data of any changes associated with elongation of the visceral hump.

Reduction in whorl count and thus in the total length of the visceral hump is a common pattern in charopids from many areas of the world. Such taxa as

the Juan Fernandez *Amphidoxa* (fig. 30a, c), New Zealand *Flammulina*, *Maoriconcha*, and *Otoconcha* (Climo, 1971a), a few of the South African *Trachycystis* (Connolly, 1939), and some New Caledonian taxa (Solem, 1961) show varying degrees of visceral hump reduction. This is carried furthest in the New Zealand *Otoconchinae* and the semslug *Ranfurlya*. Discussion of their changes is beyond the scope of this review, but the general pattern is for zonal compaction of organs in several systems (see Solem, 1966, for a discussion of this in the Thailand Helicarionidae).

In the Pacific Island Charopidae whorl reduction takes two forms—simple decrease in mean whorl count without any change in whorl profile (*Microcharopa mimula*,  $3\frac{1}{4}$ –; *Lagivala minusculus*, 3%; *Discocharopa aperta*, 3%; and *Palikirius ponapicus*, 3%) or reduction in whorl count accompanied by a drastic increase in cross-sectional areas of the body whorl (*Russatus nigrescens*,  $3\frac{1}{8}$ –; *Ba humbugi*, 3%).

Either the former taxa have not been dissected, or, in the case of *Discocharopa*, there are no close relatives known with which anatomical comparisons can be made. Thus, comments here must be restricted to the latter situation, whorl count reduction combined with whorl cross-section increment. The degree of whorl changes can be judged by comparing whorl increment rates and whorl profiles in *Kubaryiellus* and *Russatus* (fig. 89a–b, d–e) and then in *Sinployea irregularis* (Garrett, 1887) (fig. 65d–e) and *Ba humbugi* (fig. 74a–b). Anatomically, the typically trukcharopine half whorl pallial region of *Kubaryiellus* (fig. 90e) can easily be altered to the nearly square kidney (K) and one quarter whorl pallial cavity of *Russatus* (fig. 90a) by shortening and widening of the kidney, ventral flexing



of the intestinal loop, and a slight ventral movement of the arterial part of the pericardial kidney lobe over the heart (H) and principal pulmonary vein (HV). Comparing the gross genitalia (fig. 90b, f), the proportionately shortened free oviduct (UV), spermatheca (S), prostate (DG), and uterus (UT) of *Russatus* are obvious. There is no detectable change in the penis (P) and vagina (V). The pallial region of *Sinployea irregularis* (Garrett, 1887) was not illustrated, but it has the typical generic pattern of extending  $\frac{5}{8}$  of a whorl apically, there is no lung roof space visible between the arms of the ureter, and the rectal lobe is distinctly longer than the pericardial. In *Ba humbugi* (fig. 75a) the anterior half of the half whorl pallial cavity has undergone shortening and change, with the anterior margins of the kidney flared laterally, but the posterior portion of the kidney and the intestinal loops are essentially unmodified when compared with the degree of change seen in *Russatus* (fig. 90a). Contrasting the genitalia of *S. irregularis* (fig. 67a, drawn from a deeply retracted specimen) and *Ba* (fig. 75b–e, h) shows a rather drastic folding of the prostate and uterus plus altered insertion of the penial retractor muscle in the latter taxon. *Ba* also shows shortening of the vagina and spermatheca.

Thus, changes in the visceral hump length of Pacific Island Charopidae involve selective shortenings in portions of the organ systems lying in the pallial region. Unless there is clear shortening of the neck region (area between ommatophores and pallial collar edge when animal is crawling), the prostate-uterine area and spermathecal-free oviduct sections are more apt to be involved than the penis-vagina, and the kidney area, than the gas exchange surfaces of the pallial roof. More extended comments on these changes are postponed pending completion of studies on Australian and New Zealand taxa.

#### SUMMARY OF ANATOMICAL VARIATION

The Pacific Island Charopidae show a number of minor variations in the terminal genitalia and kidney configurations. The former involve species recognition factors, the latter are of uncertain significance except

in cases of obvious elongation or shortening of the pallial cavity. These terminal genitalia patterns are not continuously variable, but fall into rather discrete general patterns that indicate multiple colonizations of the island areas and are used in part to recognize sub-family units.

The major and minor anatomical differences between the Pacific Island Charopidae and Endodontidae were summarized by Solem (1976b, pp. 97–98, tables LVIII–LIX). Consideration of the complexities in the Australian, New Zealand, and New Caledonian taxa must be deferred. There are no clear unitary anatomical trends within the Pacific Island Charopidae compared with those outlined for the Endodontidae (Solem, 1976b, pp. 98–99), although the addition of structures among the various charopid subfamilies is striking.

A major correlative of the "looser" whorl coiling pattern (pp. 41–43) in the Charopidae compared with the Endodontidae is that the cross-sectional area of the body whorl in particular is greater in the former family. This has important implications on the size of the anterior body and its contained organs. The wider area in the Charopidae permits widening of the terminal genitalia. The much fatter penis and vagina-free oviduct-spermathecal union area in the Charopidae is possible directly because of this extra space provided by the looser coiling. Whereas in the Endodontidae these organs all are thin tubes, in most Charopidae they are thick and with complex internal structures.

The only Pacific Island charopid known to have clearly narrowed structures in this area is *Jokajdon callizonus* (Möllendorff, 1900) (fig. 93a–b), whose drastically narrowed shell aperture and large apertural barriers (fig. 92a) closely approach the typical endodontid condition. Even though species of *Palline* (figs. 94b, e, 95d) have large apertural barriers and somewhat narrowed apertures, the thick terminal genitalia (fig. 93f, h) contrasts with that of *Jokajdon* and is in the typical charopid pattern.

It is quite probable that the variety of genital structures seen in the Charopidae as opposed to the Endodontidae are in large part the result of simple space availability for experimentation.

# CHAROPID-ENDODONTID CONCHOLOGICAL COMPARISONS

Despite almost complete overlap with regard to most conchological characteristics and their close similarity when viewed with the naked eye, there are a few clear differences between the Endodontidae and Charopidae in meristic and structural features. Data in Tables I-III and X and Figures 15-23 summarize both similarities and differences in some basic parameters. Figures 15-22 were prepared several years ago and omit data on the Lau Archipelago endodontids, *Priceconcha tuvuthaensis* Solem (1973d) and *Thaumatonodon spirrhymatum* Solem (1973d). Their inclusion would not have changed the results significantly. In addition, four taxa of endodontids were not seen or measured. These two exceptions account for the difference between the 185 taxa listed by Solem (1976b, p. 9, table IV) and the 179 listed as measured in this tabular comparison.

For ease in visual comparison, in Figures 15-22 the actual numbers of species for each graph unit have been converted into percentages of the total measured within that family so that the graphs will be directly comparable. Otherwise the difference between 179 endodontids and 95 charopids would make visual comparisons difficult.

Table X shows the median mean value and total range of mean values for the species measured within each family. The distinctly larger size and higher whorl count of the Endodontidae is evident, whereas their near identity in H/D ratios, D/U ratios, and mean rib counts is surprising. The greater ribs/mm. in the Charopidae directly correlate with their smaller size.

TABLE X. - CONCHOLOGICAL COMPARISONS OF ENDODONTIDAE AND CHAROPIDAE FROM PACIFIC ISLANDS.

	Endodontidae	Charopidae
Number of species		
level taxa measured	179	95
Median mean height (range)	1.48(0.92-7.26)	1.51(0.48-3.69)
Median mean diameter (range)	3.77(1.7-12.3)	2.76(1.07-7.52)
Median mean whorl count (range)	5 1/2+ (3 5/8-8 1/8)	4 1/8- (3 1/8-6 5/8)
Median mean H/D ratio (range)	0.531 (0.344-0.789)	0.523 (0.365-0.801)
Median mean D/U ratio (range)	3.94 (1.68-closed)	3.94 (2.03-closed)
Median mean ribs on body whorl (range)	91.0(19-202)	91.2(19-225)
Median mean ribs/mm.	9.2(1.4-40)	11.3(1.7-37)
Taxa with ribs reduced	39(21.8%)	10(10.5%)

The greater degree of rib reduction in the Endodontidae and the reduction in percentage of taxa with apertural barriers in the Charopidae also indicate major differences.

More detailed comments can be made from the data in Figures 15-23. Mean height distribution (fig. 15) shows a slight Endodontidae offset for most species, then an extended high-spined portion that far sur-

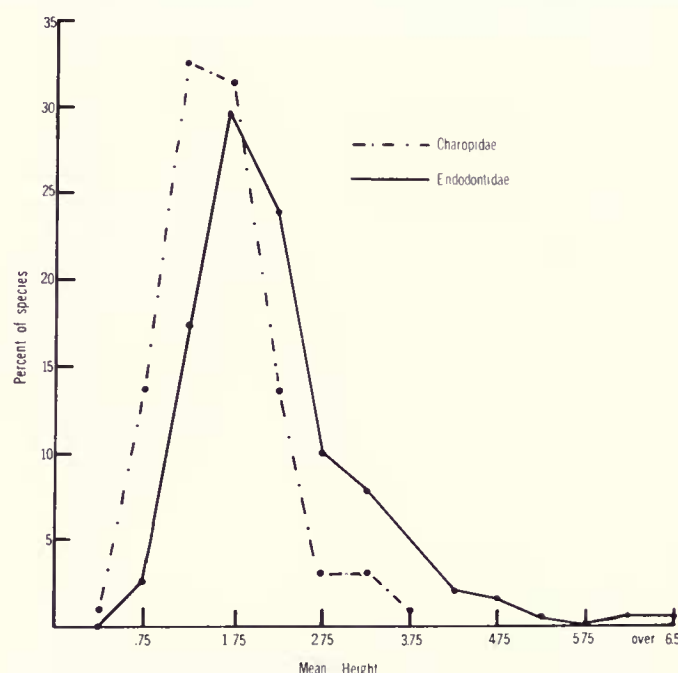


FIG. 15. Mean shell height distribution in the Endodontidae and Charopidae.

passes the maximum height recorded for the Charopidae. The three highest spired Charopidae are *Lauopa mbalavuana*, *Tuimalila infundibulus* (Hombron & Jacquinot, 1841), and *T. pilsbryi*. All three have average to only slightly increased whorl counts, and only the latter has a high SP/BWW ratio (mean 2.23). Their large height is the result of size increase alone, rather than change in shell form. In contrast, the high-shelled Endodontidae mostly are species with umbilical brood chambers and increased whorl counts, plus the few *Nesodiscus* and pre-brood chamber *Endodonta* (Solem, 1976b, pp. 27-30).

Mean diameter distribution (fig. 16) shows a greater similarity between the two families, both having a significant right extension of the frequency curve. The sharper peak for the Charopidae relates to



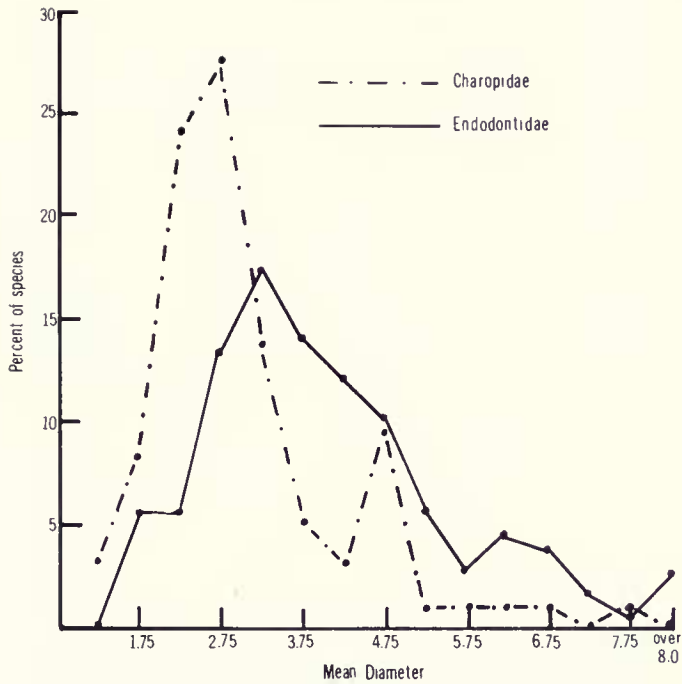


FIG. 16. Mean shell diameter distribution in the Endodontidae and Charopidae.

the speciose genus *Sinployea*, which accounts for more than half of the total taxa reviewed. The secondary peak around 4.75 mm. results from some of the large Rarotongan and Samoan *Sinployea*, plus *Himeroncha*, *Russatus*, and large *Semperdon* from Micronesia. Both families have a few taxa that exhibit gigantism compared with the average species.

Mean H/D ratio distribution (fig. 17) differs only because of the brood chamber taxa in the Endodontidae (Solem, 1976b, p. 29, fig. 19), producing a slight bulge

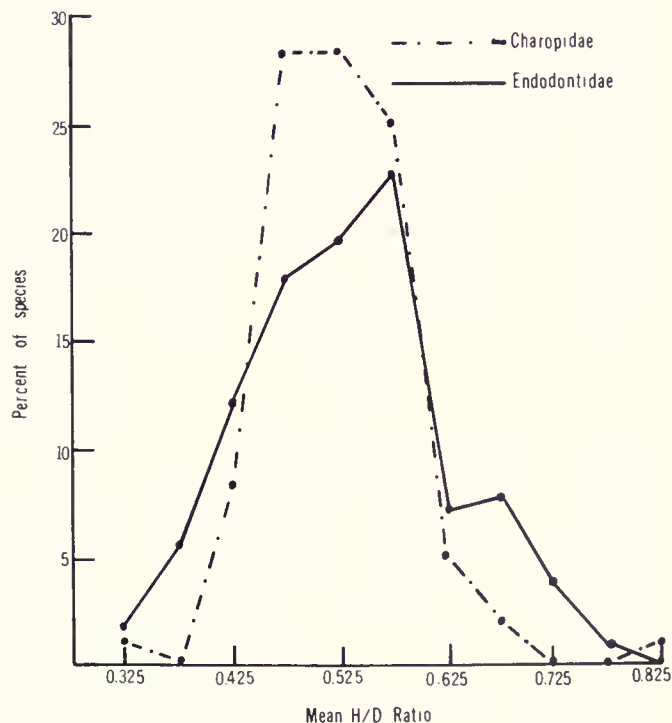


FIG. 17. Mean height/diameter ratio distribution in the Endodontidae and Charopidae.

in the higher ratios for that family. The only very high-spined charopids are the nearly scalariform *Ba humbugi* (fig. 74b), *Ladronellum mariannarum* (Quadrans & Möllendorff, 1894) (fig. 101b), and *Semperdon kororensis* (Beddome, 1889) (fig. 98b). Only *Ladronellum* has a normally open umbilicus (fig. 101c), whereas the others have a closed umbilicus that normally increases the H/D ratio dramatically (Solem, 1976b, p. 25, fig. 15).

The most dramatic difference is shown by the mean whorl count distribution (fig. 18). The only charopids to exceed a mean whorl count of five whorls

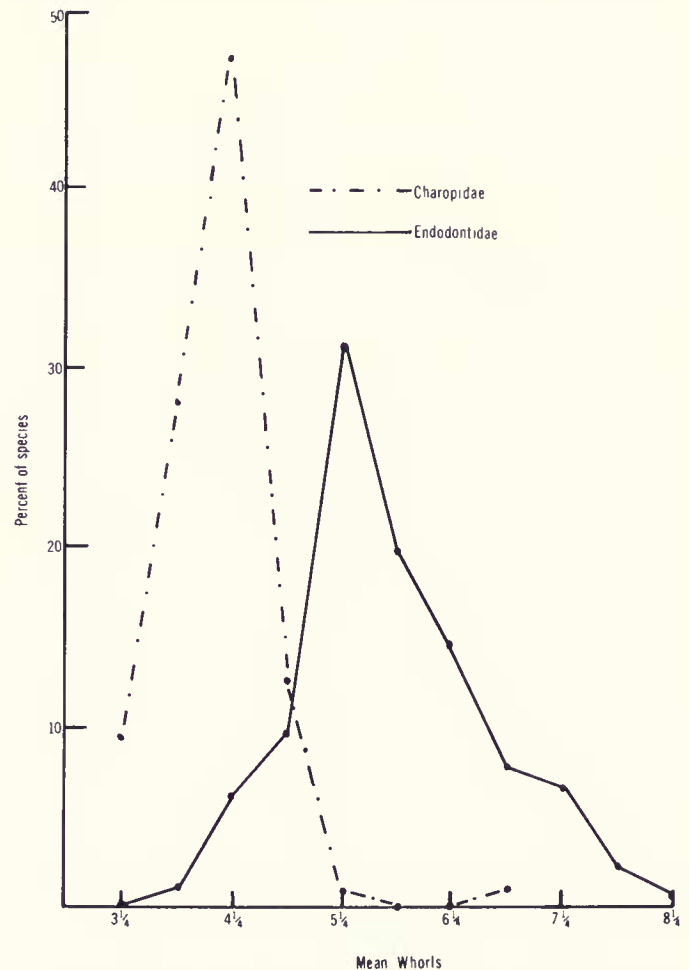


FIG. 18. Mean whorl count distribution in the Endodontidae and Charopidae.

are the Micronesian *Semperdon kororensis* (Beddome, 1889) (fig. 98a) with 5 1/8 average, and the Rarotongan *Sinployea planospira* (Garrett, 1881) (fig. 46d) with 6 5/8 whorl average. Although there is considerable overlap in mean whorl counts of five whorls or less, the dramatic increase in higher mean whorl counts in the Endodontidae is quite clear. A fair portion of this increase to the right correlates with brood chamber formation (Solem, 1976b, p. 29, fig. 20).

Means of D/U ratio for the Endodontidae in Figure 19 exclude the brood chamber taxa entirely, hence the two families show very similar patterns. Because egg laying in the umbilicus is a family characteristic in the

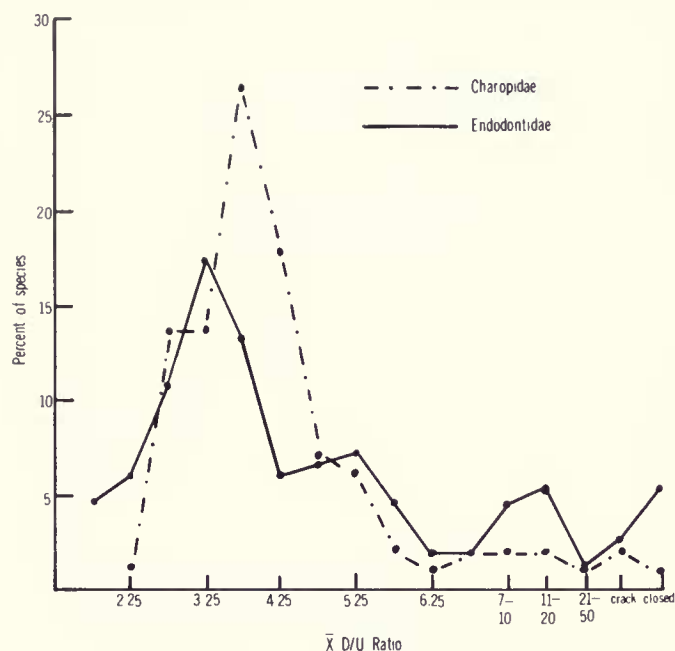


FIG. 19. Mean diameter/umbilical width ratio distribution in the Endodontidae and Charopidae.

Endodontidae (Solem, 1976b, pp. 100–101), extreme narrowing or closure of the umbilicus should be a rarer event in the Endodontidae than in the Charopidae. Surprisingly enough, it is not. The only Charopidae with a closed or nearly closed umbilicus are *Semperdon kororensis* (Beddome, 1889) (fig. 98c) from Palau, *Sinployea clista* (fig. 51c) from Samoa, and *Ba humbugi* (fig. 74c) from Viti Levu, Fiji. *Sinployea clausa* (fig. 51f) from Samoa has an extremely narrowed umbilicus. Most other species have the umbilicus much more widely opened, and only in the Lau Archipelago *Sinployea adposita* (Mousson, 1870) (fig. 69f) and *Russatus nigrescens* (Möllerndorff, 1900) (fig. 89f) from Ponape is the umbilicus very narrow. In the Endodontidae (Solem, 1976b, pp. 26, 491–492) there are 10 taxa with closed and 10 with barely perforate umbilici. Most of these are found on Rapa and Mangareva, areas far from the main areas of distribution and possibly from the natural occurrence of potential egg predators that occupy the leaf litter. Hence, the unexpected high occurrence of closed or barely perforate umbilici in the Endodontidae is a geographic phenomenon.

The degree of spire protrusion, as measured by the SP/BWW ratio, is quite different for the two families (fig. 20). The Endodontidae are in general much higher spired. This relates primarily to the taxa reaching the *Nesodiscus* and brood chamber levels of organization. The most elevated Charopidae are *Ba humbugi* from Fiji (fig. 74b), *Ladronellum mariannarum* (Quadrass & Möllerndorff, 1894) from Guam (fig. 101b), *Sinployea angularis* from Fiji (fig. 64e), and *Vatusila nayauana* from Fiji (fig. 82e). Because so few Pacific Island Charopidae have elevated spires, the type of analysis done for the Endodontidae (Solem, 1976b, p. 25, fig. 15) in which spire protrusion was correlated with varia-

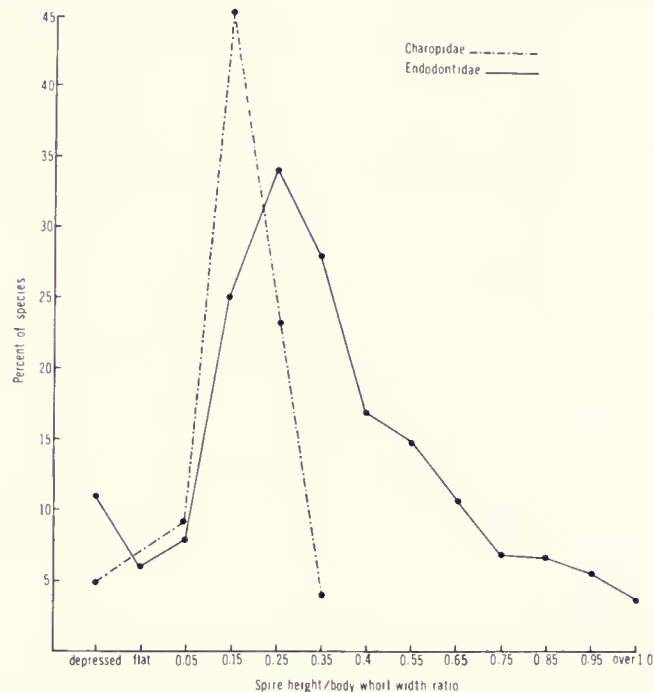


FIG. 20. Mean spire height/body whorl width ratio distribution in the Endodontidae and Charopidae.

tions in shell height, diameter, H/D ratio, and D/U ratio is not presented since the differences were so slight. Comparatively few Charopidae have a flat or clearly depressed spire. Only *Roimontis tolotomensis* has a clearly sunken spire.

The striking similarity in median mean rib counts on the body whorl (table X) and the very similar distribution of mean rib counts in the two families (fig. 21) was not anticipated. It does suggest that the hypothesized function of the ribbing to reduce adherence of particles to the shell surface (Solem, 1976b, p. 50) may be correct. Rib reduction in the Endodontidae is primarily size correlated. Species with a mean diameter of 4.75 mm. or more frequently show a marked degree of rib reduction (Solem, 1976b, pp. 46–50, tables

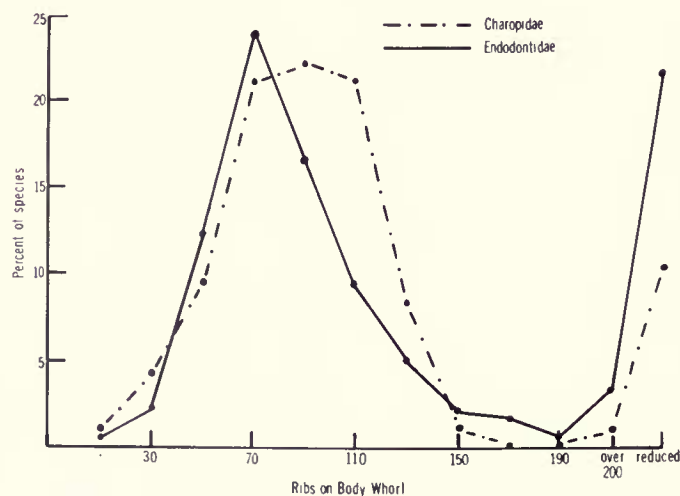


FIG. 21. Mean ribs on body whorl distribution in the Endodontidae and Charopidae.



XVII–XIX). There are comparatively few taxa in the Charopidae that show major rib reduction. The 10 are not phyletically correlated and show reduction in different degrees and ways. In *Himeroconcha rotula* (Quadras & Möllendorff, 1894) and *H. lamlanensis* from Guam, plus *Sinployea rudis* (Garrett, 1872) and *S. harveyensis* (Garrett, 1872) from Rarotonga, the sculpture is reduced to irregularity on the body whorl, with the major ribs becoming too crowded and too irregular to count well before the lip. In *Sinployea irregularis* (Garrett, 1887) and *Ba humbugi* from Fiji plus *Russatus nigrescens* (Möllendorff, 1900) from Ponape, the postapical sculpture is highly irregular, and occasionally a rib with a high lamellar extension appears. In *Sinployea recurva* from Fiji and *Himeroconcha quadras* (Möllendorff, 1894) and *H. fusca* (Quadras & Möllendorff, 1894) from Guam, the sculpture is reduced in prominence on both the spire and body whorl and rapidly becomes indistinguishable from growth lines after an initial portion where the ribs are large enough to be counted. The four *Himeroconcha* do show a pattern of size-associated reduction in rib prominence, since the two smaller species have more prominent spire sculpture (fig. 104a–f) than do the two larger taxa (fig. 105a–f). There is no data available concerning the ecology of *Himeroconcha*, so that the reasons for this pattern of sculpture reduction are unknown. *Russatus*, *Ba*, and *Sinployea irregularis* (Garrett, 1887) are known to be terrestrial in habitat, and Garrett (1872, pp. 227–228) reported that both *S. rudis* (Garrett, 1872) and *S. harveyensis* (Garrett, 1872) were collected under rotting wood. Only dead examples of the Lau Archipelago *Sinployea recurva* are known, although I have speculated that it could be an arboreal species.

The overall pattern of rib reduction in the Charopidae is less clearly size linked than in the Endodontidae. Three of the 10 species, *S. recurva*, *S. irregularis* (Garrett, 1887), and *Ba humbugi* are within 0.11 mm. of the median mean diameter, the other seven (38.9%) are among the 18 over 3.75 mm. in diameter, and three (37.5%) are among the eight species that average more than 4.75 mm. in diameter. They are *Russatus nigrescens* (Möllendorff, 1900), *Himeroconcha fusca* (Quadras & Möllendorff, 1894), and *H. quadras* (Möllendorff, 1894). In the Endodontidae, 50% of the taxa averaging over 4.76 mm. in diameter have reduced sculpture (Solem, 1976b, p. 47, table XVIII).

The variation in mean ribs/mm. on the body whorl (fig. 22) is equivalent in the two families, once allowance is made for the smaller mean size of the Charopidae. As in the Endodontidae (Solem, 1976b, pp. 44–45, tables XV–XVI), the smaller the mean diameter, in general the more numerous are the radial ribs (see table X).

In summary, basic shell size, shape, and radial sculpture spacing and frequency in both families are more similar than dissimilar, once allowance is made

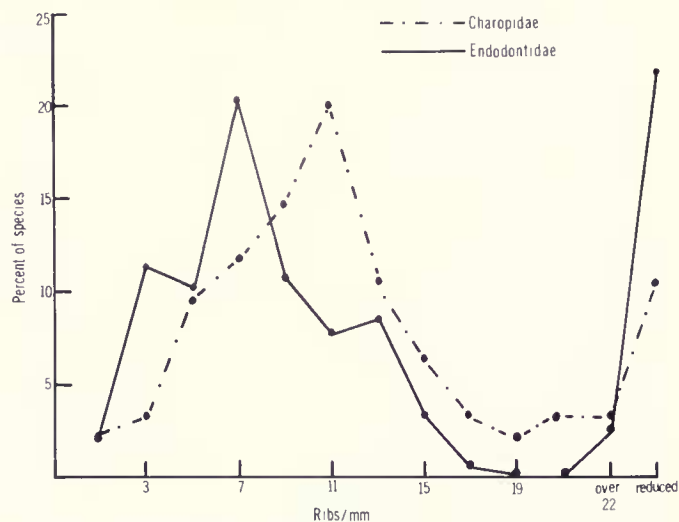


FIG. 22. Mean ribs/mm. on the body whorl distribution in the Endodontidae and Charopidae.

for the changes in the Endodontidae caused by the formation of a brood chamber. The Endodontidae are larger and with a higher whorl count than the Charopidae, but in basic form and character of the radial sculpture they are very similar. This is not surprising because both are basically found in litter, under stones, and in or under rotting wood. A much higher number of Charopidae than Endodontidae has been taken in semiarboreal to arboreal situations.

In addition to gross size, shape, and sculpture comparisons, an important question is whether there is a different pattern of growth between the two families. With the complications introduced by variations in spire protrusion, body whorl descension, umbilical width, whorl counts, and sculptural protrusions, it is difficult to find a simple index of whorl increment pattern that will at least indicate the pattern of whorl width increase. Figure 23 attempts this through use of a crude measure of size increment plotted against whorl count of the figured individual. To try and minimize difficulties in interpretation, brood chamber taxa and the very high-spined members of *Aaadonta* in the Endodontidae plus the high-spined *Ba humbugi* in the Charopidae have been omitted. Inclusion of these would have added data points to the lower right of the figure. Because the increase in shell diameter is less when the spire is elevated, the results would have been artificially skewed toward the right.

The basic data for Figure 23 were taken from the top views of shells as published in Solem (1976b) and this report. Because top views were not published for species of *Anceyodonta*, nearly all *Cookeconcha*, *Opanara*, *Rhysoconcha*, *Ruatara*, *Orangia*, *Taipidon*, *Planudonta*, *Rikitea*, and *Nesophila*, this is only a partial sampling of the Endodontidae. In contrast, nearly all of the Charopidae have been figured in top view. On each illustration, two measurements were made: the width of the first whorl from suture to suture and then the diameter of the entire shell. In addition, the

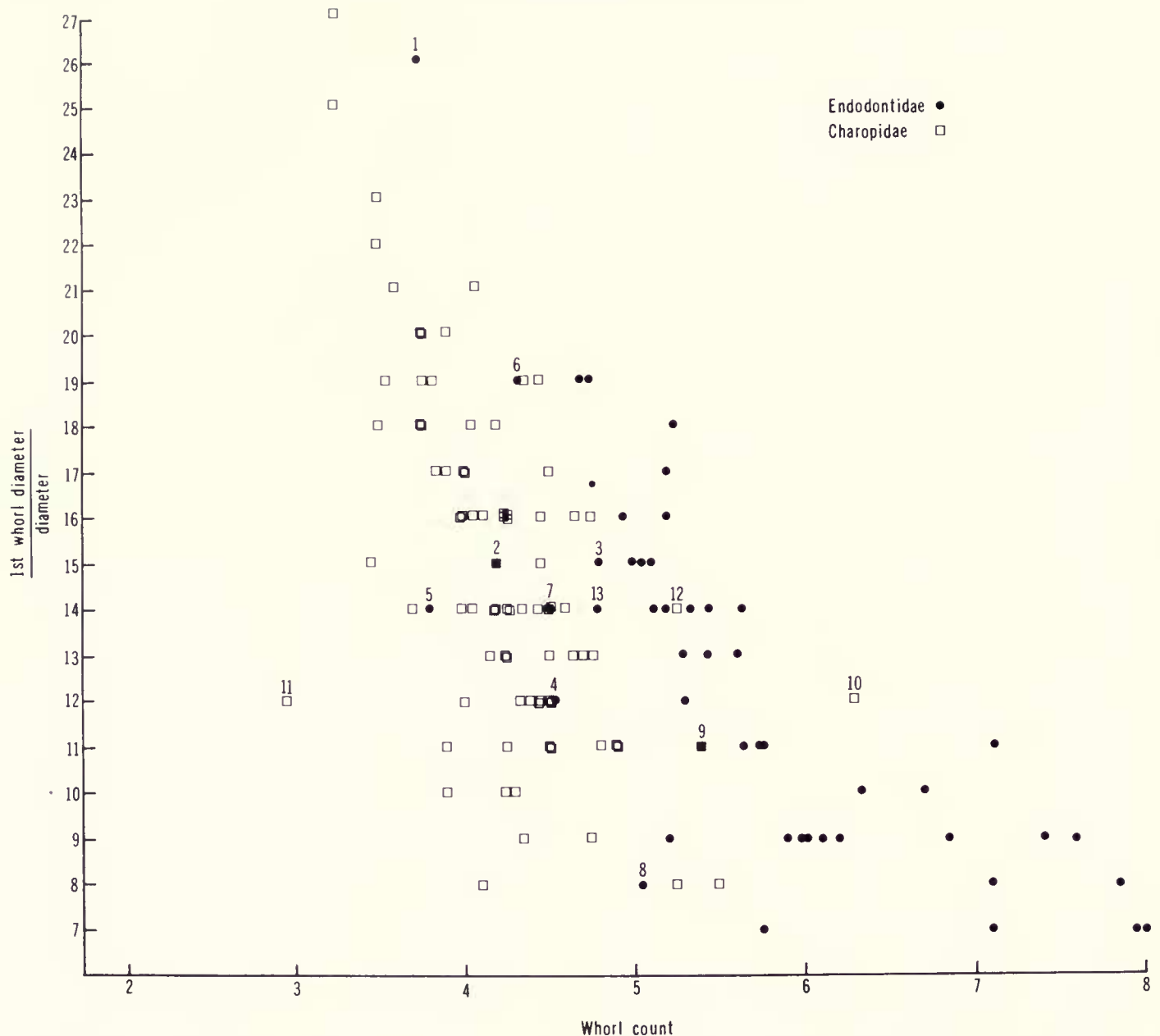


FIG. 23. Patterns of whorl width increment in selected Endodontidae and Charopidae. Brood chamber, very high spired, and unillustrated top views of species in the Endodontidae are omitted, as is the high-spired *Ba humbugi* in the Charopidae. Unusual taxa are: (1) *Minidonta manuauensis* Solem, 1976; (2) *Mautodontha aoraiensis* Solem, 1976; (3) *Australdonta pseudplanulata* Solem, 1976; (4) *A. pharcata* Solem, 1976; (5) *Cookeconcha stellulus* (Gould, 1844); (6) *Thaumatodon laddi* Solem, 1976; (7) *Zyzyxdonta alata* Solem, 1976; (8) *Aaadonta kinlochi* Solem, 1976; (9) *Sinployea canalis* (Garrett, 1872); (10) *S. planospira* (Garrett, 1881); (11) *Russatus nigrescens* (Möllendorff, 1900); (12) *Semperdon kororensis* (Beddome, 1889); and (13) *Minidonta micraconica* Solem, 1976.

number of whorls in the illustrated specimen was recorded. The width of the first whorl was divided by the total diameter to give a percentage of the total diameter taken up by the initial nuclear whorl. This is, of course, partly inaccurate, because the suture-to-suture distance will be less than the periphery-to-periphery distance. The error will be approximately the same for each species, so that the degree of error will be in the same direction. Use of a percentage index of total diameter plotted against the actual whorl count gives an approximate indication of basic whorl width increments.

It is evident that members of the Endodontidae have a tighter pattern of coiling at the same whorl count than do the Charopidae. The higher the percentage of the first nuclear whorl width, the slower is the rate of whorl width increment for succeeding whorls. There is, in general, a rather clear separation between the two family units. The exceptions from the general pattern in the Charopidae are a few species with unusual coiling patterns: (number 9 on fig. 23) *Sinployea canalis* (Garrett, 1872) (fig. 49a-c), which has a laterally compressed whorl profile and increased whorl count; (number 10) *S. planospira* (Garrett, 1881) (fig.



46d-h), which is laterally compressed, has increased whorl count, and very tight coiling; and (number 12) *Semperdon kororensis* (Beddome, 1889) (fig. 98a-c), with its raised spire, lateral compression, and closed umbilicus. At the other extreme, (number 11) *Russatus nigrescens* (Möllendorff, 1900) (fig. 89d-f), which has a flat spire, reduced whorl count, and reduced sculpture, is offset to the left considerably. The unusual Endodontidae include (number 1) *Minidonta manuaensis* Solem (1976b, p. 131, fig. 62a) and (number 13) *Minidonta micraconica* Solem (1976b, p. 138, fig. 65a-c) with reduced whorl counts and abnormally flat-spired taxa in normally more elevated genera such as (number 2) *Mautodontha aoraiensis* Solem (1976b, p. 160, fig. 74d-f), (number 3) *Australdonta pseudplanulata* Solem (1976b, p. 295, fig. 127d-f), and (number 4) *A. pharcata* Solem (1976b, p. 313, fig. 137a-c). Taxa whose diameter was increased by greatly enlarged radial ribs include (number 5) *Cookeconcha stellulus* (Gould, 1844) (Solem, 1976b, p. 218, fig. 93a-c) and (number 7) *Zyzyxdonta alata* Solem (1976b, p. 466, fig. 198a-c). *Aaadonta kinlochi* Solem (1976b, p. 486, fig. 208a-c, number 8) is a flat-spired species in a genus that is normally highly elevated, whereas (number 6) *Thaumatodon laddi* Solem (1976b, p. 452, fig. 193d-f) is a flat-spired species with slightly protruded periphery. Thus, all exceptions are readily explained as representing special situations.

Correlated with the more rapid whorl width increment in the Charopidae is a greater increase in cross-sectional area of the whorl profile. Without sectioning shells and measuring the areas of the whorls, quantification of this difference is not feasible. The fact of the greater cross-sectional area and concomitant increase in linear wall distance at any given point undoubtedly has had major effects on the placement of pallial organs in relation to each other and their length. It also has permitted thickening of genital organs over the endodontid condition. Discussion of these changes was dealt with under the patterns of anatomical variation.

On the submicroscopic level, there are three major differences between the Endodontidae and Charopidae found on the Pacific Islands. The apical sculpture of the shell, the method of forming the postapical shell sculpture, and the way in which the apertural barriers are formed and armed with microdenticles are different. These differences have been reviewed in part elsewhere (Solem, 1969d). Only a brief summary is included here.

In the Endodontidae, the apical sculpture consists of prominent radial ribs, with or without microriblets in between, plus very fine spiral cords that are best termed "squiggly" (Solem, 1976b, pp. 35-41, figs. 25-31). In one genus, *Aaadonta* Solem (1976b, pp. 38-39, figs. 28-29), the major radial sculpture has been lost, only the microradials are left on the postapical whorls, and only the squiggly spiral cords are left on the apex. In the Pacific Island Charopidae, the basic

apical sculpture is of strong spiral cords, typically as seen in *Sinployea modicella* (Férussac, 1840) (fig. 1a-c). They can be reduced in prominence and increased in number, as in *Sinployea peasei* (fig. 2a-b), or combined with a secondary sculpture of low radial swellings, as in *Tuimalila pilsbryi* (fig. 2c). The only exceptions on the Pacific Islands concern the rotadiscine genus *Microcharopa*, in which the spiral apical cords are broken up into short, twisted segments (fig. 4a-e), and the widespread *Discocharopa* (fig. 5), in which both apical and postapical sculpture consists of fine radial ribs and there is no trace of spiral sculpture. The situation becomes much more complicated in the charopid taxa of Australia and New Zealand where there have been many experiments in shell sculpture (Solem, unpublished data). However, in relation to the Pacific Island taxa, the sharp division into taxa with spiral cords (Charopidae) and taxa with radial ribs (Endodontidae) holds with a few secondary exceptions. Under optical magnification, *Aaadonta* would be confused with the charopid condition and *Tuimalila* with the endodontid condition, but SEM studies show that these apparent exceptions are secondary modifications.

Except for obvious periostracal setae and extensions in such taxa as *Cookeconcha decussatulus* (Pease, 1866) (Solem, 1976b, p. 36, fig. 26a-c; p. 40, fig. 30b), the postapical sculpture in the Endodontidae apparently is formed by a thin template of periostracum, with most of the sculpture thickness consisting of underlying calcium layers. This holds even for the fine apical features (Solem, 1976b, p. 35, fig. 25d). In contrast, the microsculpture and much of the major rib projection in the Charopidae consists entirely of periostracal materials. Frequently the only calcareous sculptural element will be a swelling underneath each major radial rib. An example of this is seen in *Sinployea vicaria vicaria* (Mousson, 1871) (fig. 59). The same pattern of structure seems to hold true for at least many of the New Zealand and Australian Charopidae. This makes the similarity in gross sculpture effect between the two families even more remarkable.

An initial review of the apertural barrier differences between the Endodontidae and Charopidae was given in Solem (1973b). The following summary is taken from that paper, Solem (1976b, pp. 52-72), and pp. 15-23. In the Endodontidae, the barriers show a uniform pattern of structure, growth, and microdenticulation. The parietal and columellar walls will have weak pustulations, as is typical of many taxa in a variety of families (Solem, 1972c), but the characteristic feature on the barrier tops is a series of additive triangular microdenticulations (Solem, 1973b, figs. 7-13, 23-24; Solem, 1976b, p. 55, fig. 39d-e; p. 64, figs. 40, 41a-c). It apparently does not matter whether the expanded upper edge of the barrier is continuous or broken up into a series of expanded beads as in *Thaumatodon*, *Aaadonta*, and *Zyzyxdonta* (Solem, 1976b, p. 457, fig. 194b-e; p. 466, fig. 198b; p. 475, fig. 203b, e). The pattern of minute triangular denticles

that face toward the aperture and are additions to the surface of the barrier, rather than an outgrowth from it, holds. The only known exceptions are in certain of the very large species of *Cookeconcha* and *Endodonta*, where the denticulations on the upper edge of the barriers are blunt-tipped (Solem, 1976b, p. 66, fig. 42d–f) although retaining their triangular shape on the sides of the barriers, and in other genera such as *Nesodiscus*, where the barriers are greatly reduced in both size and number. These barriers may be secondarily without denticulations. I have thus concluded that the barriers seen in members of the Endodontidae had a common origin and that reduction or loss of barriers is a secondary phenomenon in that family.

In the Charopidae (pp. 15–17), in contrast, three of the four major groups with barrier-equipped genera found on the Pacific Islands show barriers that differ in size, position, growth, and microdenticulations (Solem, 1973b, pp. 303–304, figs. 4–6, 14–22). The latter basically are crystals growing out of the barrier surface and are blunt tipped. It is thus concluded that apertural barriers have evolved independently in each of these lineages, despite the fact that SEM observations could not be made on the *Sinployea*-derivative genera. Their barriers show such obvious differences from the other three groups (figs. 80–83, 85) that I have no doubt of their independent origin. More detailed discussion of the barrier structure and variation has been

given in the Patterns of Morphological Variation (pp. 15–23).

In the Endodontidae the great majority of the species have barriers on the palatal wall, with a bladelike shape and gradual anterior descension. In the Charopidae only four species have bladelike palatal barriers, and 13 have purely crescent-shaped barriers.

The frequency of barrier occurrence is lower in the Charopidae than in the Endodontidae. In the latter, including taxa not seen but illustrated in older literature, 184 out of 185 (99.5%) have parietal barriers and 163 (88.1%) have palatal barriers. In the Charopidae 32 (33.7%) of 95 taxa have parietals, and 27 (28.4%) have palatal barriers. Thus the families differ significantly not only in whether or not barriers are present in the aperture but also in how they are formed, the normal shape of the palatals, and the nature of the microdenticulations on the barrier edges.

Despite great optical similarity in size, color, shape, presence of apertural barriers in many species, and presence of fine radial ribbing in at least the smaller taxa, differences in whorl count (fig. 18), growth pattern of whorl width (fig. 23), apical sculpture, method of formation for the postapical sculpture, and details of the apertural barrier structure and microdenticulations serve to distinguish the two families on conchological grounds.



## HABITAT RANGE AND EXTINCTION

In contrast with the Endodontidae (Solem, 1976b, pp. 100–101), the Charopidae have been able to exploit the semiarboreal and arboreal habitats as well as remaining well represented in the ground stratum. Their closed secondary ureter has been hypothesized (Solem, 1976b, p. 100) as the reason the charopids have been able to become successfully semiarboreal. A second factor in their success is the apparent lack of umbilical egg deposition by the charopids. Of all the Pacific Island charopid specimens studied, only one example of *Tuimalila infundibulus* (Hombron & Jacquinet, 1841) had a snail egg capsule inside the umbilicus, whereas this is the routine pattern in the Endodontidae. Of extralimital taxa, the New Zealand charopids, *Fectola marsupialis* Powell, 1941, and *Aeschrodomus worleyi* Powell, 1928, have the umbilical egg-laying pattern (see Climo, 1969a, pp. 218–219; 1970, p. 306).

On such drastically ecologically altered islands as Viti Levu, Tahiti, and Moorea, specimens of *Sinployea* and *Ba* have been collected from lowland vegetational remnants in the 1960s and 1970s. They have not, however, been found where the ground stratum has been severely and regularly disturbed by chickens and/or pigs. In parts of Samoa and on the Lau Archipelago of Fiji the charopids still are common and relatively abundant. Only on Rarotonga is there clear evidence of major charopid extinctions within a century. Two separate collecting efforts on Rarotonga in the mid-1960s failed to find nine out of 10 *Sinployea* species collected in the 1860s and 1870s and five out of six endodontids reported from the same island. All of the missing taxa were described as ground stratum inland species. The

one collected endodontid occupies the storm line coral boulder habitat, and the one previously described *Sinployea* is at least occasionally semiarboreal.

The actual egg-laying habits of the Pacific Island Charopidae are unknown, but their nondependence upon the umbilicus for egg-laying probably has effectively lowered ant predation, which apparently was a major factor in the mass extinction of the Pacific Island Endodontidae. The semiarboreal to arboreal habitat range extension of the Charopidae also has lessened human impact through introductions, because arboreal snails of the Pacific Islands, in general, have been able to adapt to plantations of bananas and even coffee, whereas strictly ground-dwelling taxa are absent from these human-introduced environments.

The charopids are abundant in Australia, South Africa, New Zealand, New Caledonia, and parts of South America—all areas in which ants are common. I thus expect that the ability of the Pacific Island charopids to survive despite the introduction of predacious ants is a carryover from conditions in their areas of greater abundance rather than a new adaptation. Since ants first appeared in the Cretaceous fossil record (Wilson et al., 1967), and have an extensive fossil record of living tribes and genera from the Oligocene and Miocene, their coexistence with the basic charopid stock seems highly probable.

The charopids thus occupy a wider range of habitats than do the Endodontidae and persist in fair variety despite the great ecological alterations of the past century on the Pacific Islands.

## PHYLOGENY AND CLASSIFICATION

Reviews of the hypothesized early evolution and progressive trends among land snails have been given previously (Solem, 1974; 1976b, pp. 102–104; 1978b). The position of the Endodontidae as the most generalized extant group of the Sigmurethra, the absence of any family unit from which the endodontid anatomical structures can be derived, and the positioning of both the Charopidae and Endodontidae within the Arionacea complex have been discussed earlier and will not be rejustified here.

The Charopidae are more advanced than the Endodontidae in having a closed secondary ureter, fused prostate-uterine tubes with a common lumen, a reduced number of lobes in the ovotestis, and in transferring sperm in a packet (see *Ba humbugi*, fig. 75f–g), which correlates with the general presence of an epiphallus. Charopids are more complex than the En-

dodontidae in having great elaboration of terminal genital structures and in the variety of their radular structures. Recent dissections of some undescribed Western Australian taxa have revealed genera that are partly transitional between the Endodontidae and Charopidae. These will be described and discussed elsewhere.

It is premature to discuss in detail the probable phylogenetic relationships among the endodontoid families. After synoptic coverage of the Austro-Zelandic taxa, such a discussion will be profitable. At this time I choose to end the discussion of interfamily phylogeny by emphasizing that the Charopidae are more advanced than and derivable from the Endodontidae. The phylogenetic position of the Punctidae in relation to the other families is still uncertain.



## FAMILY CLASSIFICATION OF THE ENDODONTOIDS

A list of subfamily and family names available for members of this complex was given in Solem (1976b, p. 105). I recognize five families and group the assignable names as below. The name Patulinae Tryon (1866, p. 243) is discarded (see Solem, 1976b, p. 105). The affinities of the Indian Thysanotinae Godwin-Austen, 1907, are still unknown. Available literature information on their anatomy is not adequate, and I have not been able to obtain preserved materials for dissection. I have not dissected one of Iredale's family units, the Hedleyoconchidae, but on the basis of shell structures have no hesitation in lumping it with the Charopidae pending further study. Definitions and discussion of the Helicodiscidae (see Solem, 1975) and Discidae (Solem, in preparation A) are not included here, since both families are extralimital to this study. Definitions of both the Punctidae and Charopidae are included below in the systematic review; the Endodontidae were defined by Solem (1976b, p. 121).

The proposed synonymization of family level units, in chronological order, is:

- Family Punctidae (Morse, 1864, p. 27)
  - + Laominae Suter (1913, p. 732)
  - + Paralaomidae Iredale (1941a, p. 263)
- Family Charopidae Hutton (1884b, p. 199)
  - + Phenacohelicidae Suter (1892a, p. 270)
  - + Otoconchinae Cockerell (1893, pp. 188, 205)
  - + Flammulinidae Crosse (1894, p. 210)
  - + Rotadiscinae H. B. Baker (1927, pp. 226, 230)
  - + Amphidoxinae Thiele (1931, p. 575)

- + Dipnelicidae Iredale (1937b, pp. 22–23)
- + Hedleyoconchidae Iredale (1942, pp. 34–35)
- + Pseudocharopidae Iredale (1944, p. 312)
- Family Endodontidae Pilsbry, 1895 (Pilsbry, 1893–1895, p. xxviii)
- Family Helicodiscidae Pilsbry, 1927 (*in* Baker, 1927, pp. 226, 230)
  - + Stenopylinae Thiele (1931, p. 569)
- Family Discidae Thiele (1931, p. 578)
  - + Goniodiscinae Wagner (1927, p. 305)

Although I do not accept strict nomenclatural priority for names of families and higher level taxa, the above usage comes close to following this precept. I reject both Patulinae Tryon (1866) and Goniodiscinae (Wagner, 1927); the former name because *Patula* mostly has been associated with members of the land snail family Oreohelicidae, a totally unrelated group, until finally assigned as a synonym of *Discus*. *Goniodiscus* Fitzinger, 1833, is now ranked as a subgenus or synonym of *Discus* (see discussion by Forcart, 1957), and I consider it inappropriate to use as a family-level name.

The morphological gaps between these families are of the same order of magnitude or greater than the gaps separating recognized families of the Limacacea (see Solem, 1976b, p. 107), although the gaps between the family units certainly are not equal in size.

Discussion of subfamily and generic units is deferred to the family discussions of the Punctidae and Charopidae.

## PHYLOGENETIC PROCEDURES

I am a pragmatic phylogeneticist in the sense of Mayr and have used neither Hennigian cladistics nor phenetic manipulations in this study. The criteria used are those cited by Solem (1976b, p. 108) and the three-tiered approach to evolutionary change outlined in Solem (1978b). These are suited to the peculiarities of molluscan shell growth, with the ontogenetic development from embryo on visible in old age, the water-dependent ecology of land snails, and their use of terminal genitalia for species recognition.

The absence of many fixed reference points within the snail's body and the difficulties of making precise and meaningful measurements on the shell combine to make quantification of many features impossible and thus use of the more sophisticated mathematical manipulations of data matrices impractical. Similarly, in the absence of equivalently detailed analyses of most other land snail families and with the uncertainty as to the overall phylogeny of either characters or taxa, use of cladistic methodology is premature.



## GENERIC CLASSIFICATION

The same type of "pigeon-hole" generic units cited for the Endodontidae (Solem, 1976b, pp. 118–119) existed for the Pacific Island Charopidae. If there were apertural barriers present, the species was referred to the form genus *Endodonta* or to one of its sections, and if there were no such barriers present, it was placed in the New Zealand genus *Charopa*. Although Pilsbry (1893–1895, p. 21) had pointed out the artificiality of this division, no significant changes were introduced subsequently. Reference of a new species to *Flamulina* (*Russatus nigrescens*) by Möllendorff (1900) or attempts to use other described genera than *Charopa* (Solem, 1959a, 1960) did not alter the essential absence of any meaningful classification on the generic level.

Of the 21 genera in the Punctidae and Charopidae reviewed below, only two, *Punctum* and *Discocharopa*, have available names. The other 19 are named here. The same criteria for generic separation are used here in the Charopidae as were used in classifying the Endodontidae into genera (see Solem, 1976b, pp. 119–120). Thus the generic concepts are directly comparable and the minimum generic gap equally applied. The difference in frequency of monotypic genera in the two families and presence of one particularly speciose genus in the Charopidae was summarized by Solem (1976b, p. 120). This is a real difference in evolutionary patterns and not an artifact of classification.

# SYSTEMATIC REVIEW

Because the two families are so disparate in the number of species reviewed and the complexities of charopid classification require considerable reference to extralimital taxa, the discussion of charopid phylogeny and classification is subtended to the family review.

Following are a formal list of the taxa reviewed and geographic keys to the genera. These sections follow the format used in Solem (1976b) as do the species and generic accounts.

## LIST OF THE TAXA

### Family Punctidae Morse (1864, p. 27)

#### Genus *Punctum* Morse, 1864

*Punctum* sp.—Society Islands: Tahiti, Mt. Aorai  
*Punctum palynesticum*, new species—Austral Islands: Tubuai, Raivavae

### Family Charopidae Hutton (1884b, p. 199)

#### Subfamily Rotadiscinae H. B. Baker (1927, pp. 226, 228)

#### Genus *Microcharopa*, new genus

*Microcharopa mimula*, new species—Fiji Islands: Viti Levu; Lau Archipelago (Munia, Mothe, Wangava, Nayau, Namuka, Yangasa Levu)

#### Subfamily Charopinae Hutton (1884b, p. 199)

#### Genus *Discocharopa* Iredale, 1913

*Discocharopa aperta* (Möllendorff, 1888)—Philippines, Indonesia, New Guinea, Western Australia, Northern Territory, Queensland, Bismarck Archipelago, New Hebrides, Fiji Islands, Samoan Islands, Austral Islands (Rurutu), Society Islands (Borabora)

#### Genus *Sinployea*, new genus

*Sinployea modicella* (Férussac, 1840)—Society Islands: Moorea  
*Sinployea tahitiensis*, new species—Society Islands: Tahiti  
*Sinployea lamellicosta* (Garrett, 1884)—Society Islands: Tahiti  
*Sinployea montana*, new species—Society Islands: Tahiti  
*Sinployea neglecta*, new species—Society Islands: Huahine  
*Sinployea* sp.—Society Islands: Borabora  
*Sinployea atiensis* (Pease, 1870)—Cook Islands: Atiu, Aitutaki  
*Sinployea andrewi*, new species—Cook Islands: Mangaia  
*Sinployea peasei*, new species—Cook Islands: Rarotonga  
*Sinployea avanaensis*, new species—Cook Islands: Rarotonga  
*Sinployea proxima* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea planospira* (Garrett, 1881)—Cook Islands: Rarotonga  
*Sinployea rudis* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea decorticata* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea harveyensis* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea youngi* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea canalis* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea otareae* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea tenuicostata* (Garrett, 1872)—Cook Islands: Rarotonga  
*Sinployea clausa*, new species—Samoan Islands: Manu'a Group (Tau)

*Sinployea clista*, new species—Samoan Islands: Tutuila, Upolu  
*Sinployea aunuuana*, new species—Samoan Islands: Aunuu off Tutuila, possibly Manu'a Group (Tau)  
*Sinployea allecta allecta* (Cox, 1870)—Samoan Islands: Upolu, Savai'i  
*Sinployea allecta tauensis*, new subspecies—Samoan Islands: Manu'a Group (Tau)  
*Sinployea complementaria* (Mousson, 1865)—Samoan Islands: Upolu  
*Sinployea intermedia*, new species—Swains Island  
*Sinployea vicaria vicaria* (Mousson, 1871)—Hoorn Islands: Futuna; Tonga Islands: Vava'u, Tongatapu, Eua, Ha'apai Group  
*Sinployea vicaria paucicosta*, new subspecies—Tonga Islands: Vava'u  
*Sinployea rotumana* (Smith, 1897)—Rotuma  
*Sinployea ellicensis ellicensis*, new species and subspecies—Ellice Islands: Funafuti  
*Sinployea ellicensis nukulaelaeana*, new subspecies—Ellice Islands: Nukulaelae  
*Sinployea pseudavicaria*, new species—Ellice Islands: Vaitupu  
*Sinployea kusaiana*, new species—Caroline Islands: Kusaie  
*Sinployea* sp.—Mariana Islands: Saipan (possibly introduced)  
*Sinployea angularis*, new species—Fiji Islands: Lau Archipelago (Namuka)  
*Sinployea recursa*, new species—Fiji Islands: Lau Archipelago (Wangava)  
*Sinployea princei* (Liardet, 1876)—Fiji Islands: Taveuni, Kandavu  
*Sinployea inermis inermis* (Mousson, 1870)—Fiji Islands: Lau Archipelago (Vanua Mbalavu, Mango, Kimbombo)  
*Sinployea inermis meridionalis*, new subspecies—Fiji Islands: Lau Archipelago (Yangasa Levu, Navutu-i-Loma, Aiwa)  
*Sinployea inermis lakembana*, new subspecies—Fiji Islands: Lau Archipelago (Lakemba)  
*Sinployea lauensis*, new species—Fiji Islands: Lau Archipelago (Nayau, Yangasa Levu, Navutu-i-Loma, Wangava)  
*Sinployea navutuensis*, new species—Fiji Islands: Lau Archipelago (Navutu-i-Loma, ? Oneata)  
*Sinployea adposita* (Mousson, 1870)—Fiji Islands: Lau Archipelago (Oneata, Mothe, Munia, Lakemba, Aiwa, Karoni, Nayau, Yangasa Levu)  
*Sinployea irregularis* (Garrett, 1887)—Fiji Islands: Viti Levu  
*Sinployea godeffroyana*, new species—Fiji Islands: Viti Levu  
*Sinployea euryomphala* (Solem, 1959)—New Hebrides: Espiritu Santo, Maewo, Gaua, Vanua Lava  
*Sinployea solomonensis* (Clapp, 1923)—Solomon Islands: Ugi Island off San Cristobal  
*Sinployea kuntzi* (Solem, 1960)—Solomon Islands: Florida Island off Tulagi  
*Sinployea nissani* (Dell, 1955)—Solomon Islands: Nissan (Green Island), north of Bougainville  
*Sinployea novopommerana* (Rensch, 1937)—Bismarck Archipelago: New Britain  
*Sinployea descendens* (Rensch, 1937)—Bismarck Archipelago: New Britain

#### Genus *Ba*, new genus

*Ba humbugi*, new species—Fiji Islands: Viti Levu

#### Genus *Maafu*, new genus

*Maafu thaumasius*, new species—Fiji Islands: Lau Archipelago (Nayau)



Genus *Lauopa*, new genus

*Lauopa mbalavuana*, new species—Fiji Islands: Lau Archipelago (Vanua Mbalavu)

Genus *Tuimalila*, new genus

*Tuimalila infundibulus* (Hombron & Jacquinot, 1841)—Tonga Islands: Vava'u

*Tuimalila pilsbryi*, new species—Tonga Islands: Eua

Genus *Lagivala*, new genus

*Lagivala davidi* (Ladd, 1968)—Ellice Islands: Funafuti (fossil)

*Lagivala vivus*, new species—Fiji Islands: Viti Levu

*Lagivala minusculus*, new species—Fiji Islands: Viti Levu

*Lagivala macroglyphis* (Rensch, 1937)—Bismarck Archipelago: New Britain

*Lagivala microglyphis* (Rensch, 1937)—Bismarck Archipelago: New Britain

*Lagivala demani* (Tapparone-Canefri, 1883)—Indonesia (Timor, Ambon, Aru Islands); West Irian (Misool)

Genus *Vatusila*, new genus

*Vatusila kondoi*, new species—Fiji Islands: Lau Archipelago (Nayau)

*Vatusila nayauana*, new species—Fiji Islands: Lau Archipelago (Nayau)

*Vatusila eniwetokensis* (Ladd, 1958)—Marshall Islands: Eniwetok (fossil)

*Vatusila tongensis*, new species—Tonga Islands: Eua

*Vatusila vaitupuensis*, new species—Ellice Islands: Vaitupu

*Vatusila niueana*, new species—Niue Island

Genus *Graeffedon*, new genus

*Graeffedon graeffei* (Mousson, 1869)—Samoan Islands: Upolu

*Graeffedon savaiiensis*, new species—Samoan Islands: Savai'i

*Graeffedon pricei*, new species—Tonga Islands: Tongatapu

## Subfamily Trukcharopinae, new subfamily

Genus *Trukcharopa*, new genus

*Trukcharopa trukana*, new species—Caroline Islands: Truk, Lukunor

Genus *Kubaryellus*, new genus

*Kubaryellus kubaryi* (Möllerndorff, 1900)—Caroline Islands: Ponape

Genus *Russatus*, new genus

*Russatus nigrescens* (Möllerndorff, 1900)—Caroline Islands: Ponape

Genus *Roimontis*, new genus

*Roimontis tolotomensis*, new species—Caroline Islands: Ponape

Genus *Palikirus*, new genus

*Palikirus cosmetus*, new species—Caroline Islands: Ponape

*Palikirus ponapicus* (Möllerndorff, 1900)—Caroline Islands: Ponape

Genus *Jokajdon*, new genus

*Jokajdon tumidulus* (Möllerndorff, 1900)—Caroline Islands: Ponape

*Jokajdon callizonus* (Möllerndorff, 1900)—Caroline Islands: Ponape

Genus *Palline*, new genus

*Palline notera notera*, new species and subspecies—Palau Islands: Peleliu

*Palline notera palauana*, new subspecies—Palau Islands: Koror

*Palline notera gianda*, new subspecies—Palau Islands: Babelthup

*Palline biakensis*, new species—West Irian: Biak

*Palline micramyla*, new species—Caroline Islands: Ponape

## Subfamily Semperdoninae, new subfamily

Genus *Semperdon*, new genus

*Semperdon uncatus*, new species—Palau Islands: Angaur, Aulup-tagel, Koror

*Semperdon xyleborus*, new species—Palau Islands: Angaur, Koror, Ngemelis, Peleliu

*Semperdon kororensis* (Beddome, 1889)—Palau Islands: Koror

*Semperdon rotanus*, new species—Mariana Islands: Rota, northern tip of Guam

*Semperdon heptaptychius* (Quodras & Möllerndorff, 1894)—Mariana Islands: Guam

Genus *Ladronellum*, new genus

*Ladronellum mariannarum* (Quodras & Möllerndorff, 1894)—Mariana Islands: Guam

Genus *Himeroconcha*, new genus

*Himeroconcha lamlanensis*, new species—Mariana Islands: Guam

*Himeroconcha rotula* (Quodras & Möllerndorff, 1894)—Mariana Islands: Guam

*Himeroconcha quadrasi* (Möllerndorff, 1894)—Mariana Islands: Guam

*Himeroconcha fusca* (Quodras & Möllerndorff, 1894)—Mariana Islands: Guam

*Incertae sedis*

*Helix filiola* Férussac, 1840—Tonga Islands

*Helix oceanica* Le Guillou, 1842—Society Islands: Tahiti

*Helix minutialis* Deshayes, 1851—Society Islands: Tahiti

*Helix multispinata* Hombron & Jacquinot, 1852—Tonga Islands: Vava'u

*Helix rotula* Hombron & Jacquinot, 1852 (not Lowe, 1831)—Gambier Islands: Mangareva

*Pithys verccunda* Pease, 1870—Marquesas

## GEOGRAPHIC KEYS TO THE GENERA

The following artificial keys supplement those presented for the Endodontidae in Solem (1976b, pp. 124–126). They are designed to enable identification of adult shells. Endodontid taxa are cross-referenced below but usually are not keyed down to the generic level in order to save space and printing costs. Because there are no charopids or punctids known from the Mangareva, Marquesas, Rapa, or Tuamotu Islands, these areas are not included in this set of keys; nor are keys presented for extralimital areas. Additions to this set of keys are the Caroline, Mariana, and main Fijian Islands. For islands not included in the main groups, reference to the list of "odd island" taxa at the end of the keys may help.

## AUSTRAL ISLANDS

1. Apical whorls with radial ribs.....2  
Apical whorls with spiral cords.....  
*Punctum polynesianum* (p. 58)
2. Shell minute, diameter less than 1.8 mm.; at most 1 deeply recessed parietal barrier .....  
*Discocharopa aperta* (Möllerndorff, 1888) (p. 76)  
Shell normally much more than 1.8 mm. in diameter; usually several apertural barriers.....  
Endodontidae (Solem, 1976b, p. 125).

## CAROLINE ISLANDS

1. Aperture without barriers.....2  
Aperture with 1 or more barriers.....6
2. Whorls increasing rapidly in width (fig. 89d); mean D/U ratio about 10; mean whorl count about 3½ .....  
*Russatus nigrescens* (Möllerndorff, 1900) (p. 215)  
Whorls increasing less rapidly in width (fig. 89a); mean D/U ratio 3.40–4.00; mean whorl count usually more than 3½. ....3

3. Truk or Kusaie.....4  
Ponape.....5
4. Kusaie; spire elevated (fig. 63a); mean rib count on body whorl about 91.....*Sinployea kusaieana* (p. 143)  
Truk; spire barely elevated (fig. 63d); mean rib count on body whorl about 150.....*Trukcharopa trukana* (p. 208)
5. Spire flat or sunken; ribs on body whorl about 132; mean diameter about 3.75 mm. ....  
*Kubaryiellus kubaryi* (Möllerndorff, 1900) (p. 212)  
Spire slightly elevated; ribs on body whorl about 46; mean diameter about 2.2 mm. ....  
*Palikirus ponapicus* (Möllerndorff, 1900) (p. 221)
6. No columellar or palatal barriers .....7  
Palatal and/or columellar barriers present .....8
7. Only 1 parietal barrier; spire elevated; 25 large ribs on body whorl.....*Palikirus cosmetus* (p. 219)
8. Parietal barriers 2; spire sunken; about 60 low ribs on body whorl.....*Roimontis tolotomensis* (p. 217)  
Parietal and palatal barriers many and large. ....9  
Barriers consist of 1 low parietal, 2 low palatals. ....  
*Palline micramyla* (p. 234)
9. Spire more elevated; ribs larger; body whorl rounded (fig. 92e).....*Jokajdon tumidulus* (Möllerndorff, 1900) (p. 223)  
Spire barely elevated; ribs smaller; body whorl laterally compressed behind aperture (fig. 92b).....  
*Jokajdon callizonus* (Möllerndorff, 1900) (p. 226)

## COOK ISLANDS

1. Apical whorls with radial ribs; at least 1 apertural barrier.....  
Endodontidae (Solem, 1976b, p. 125)  
Apical whorls with spiral cords; no apertural barriers.....  
*Sinployea*, key on p. 98

## ELLICE ISLANDS

1. Apical whorls with spiral cords.....2  
Apical whorls with radial ribs.....  
Endodontidae, *Thaumatodon decemplicata* (Mousson, 1873)  
(Solem, 1976b, p. 451)
2. Aperture with barriers. ....3  
Aperture without barriers.....*Sinployea*, see p. 134
3. Vaitupu; living; 3 small barriers. ....  
*Vatusila vaitupuensis* (p. 196)  
Funafuti; fossil; 6 large barriers. ....  
*Lagivala davidi* (Ladd, 1968) (p. 184)

## FIJI, MAIN ISLANDS

1. Apical whorls with spiral cords.....2  
Apical whorls with radial ribs.....  
*Discocharopa aperta* (Möllerndorff, 1888) (p. 76)
2. Aperture without barriers .....3  
Aperture with barriers. ....5
3. Diameter less than 1.3 mm ..... *Microcharopa mimula* (p. 71)  
Diameter more than 2.0 mm. ....4
4. Spire greatly elevated (fig. 74b); umbilicus closed.....  
*Ba humbugi* (p. 172)  
Spire nearly flat or slightly elevated; umbilicus open.....  
*Sinployea*, see key on p. 147
5. Parietal barriers 3; D/U ratio about 2.80; ribs on body whorl about 62.....*Lagivala vivus* (p. 185)  
Parietal barrier 1; D/U ratio about 5.25; ribs on body whorl about 120. ....  
*Lagivala minusculus* (p. 185)

## HAWAIIAN ISLANDS

1. Apical whorls with radial ribs, or, in larger species, smooth.....  
Endodontidae (Solem, 1976b, p. 125)

- Apical whorls with spiral cords; shell minute.....  
*Punctum horneri* (Ancey, 1904) (p. 57)

## LAU ARCHIPELAGO, FIJI

1. Apical whorls with radial ribs.....2  
Apical whorls with spiral cords.....3
2. Several apertural barriers; diameter more than 2.5 mm. ....  
Endodontidae (Solem, 1976b, p. 125)  
One or no apertural barriers; diameter less than 2 mm.....  
*Discocharopa aperta* (Möllerndorff, 1888) (p. 76)
3. Aperture without barriers .....4  
Aperture with 1 or more barriers.....6
4. Diameter more than 2.0 mm. ....5  
Diameter less than 1.3 mm. ....*Microcharopa mimula* (p. 71)
5. Periphery protruded into a threadlike keel (fig. 76b); ribs on body whorl about 44 and very large.....  
*Maafu thaumasius* (p. 176)  
Periphery at most angulated (fig. 68e); ribs reduced in size and usually more numerous .....*Sinployea*, see key on p. 147
6. Diameter less than 2.0 mm. ....7  
Diameter more than 7.0 mm.; 1 parietal barrier. ....  
*Lauopa mbalavuana* (p. 177)
7. Palatal barriers 3; parietal barrier bifid. ....  
*Vatusila kondoi* (p. 192)  
Palatal barrier 1; parietal barrier simple.....  
*Vatusila nayauana* (p. 194)

## MARIANA ISLANDS

1. Aperture without barriers.....2  
Aperture with barriers. ....3
2. Shell small, diameter less than 2.5 mm.; Saipan.....  
*Sinployea* sp. (p. 145)  
Shell large, 3.8–7.2 mm.; Guam. ....*Himeroconcha* (p. 259)
3. Aperture with 3 very small barriers (fig. 101b).....  
*Ladronellum mariannarum* (Quadrans & Möllerndorff, 1894)  
(p. 255)  
Aperture with 6 to many barriers (fig. 99b, d–e).....  
*Semperdon rotanus* and *S. heptaptychius* (Quadrans & Möllerndorff, 1894) (pp. 245, 247)

## MARSHALL ISLANDS

1. Apical whorls with spiral cords.....  
*Vatusila eniwetokensis* (Ladd, 1958) (p. 195)
2. Apical whorls with radial ribs.....  
Endodontidae (Solem, 1976b, p. 125)

## PALAU ISLANDS

1. Postapical whorls with microradial riblets only, no major radial ribs.....Endodontidae, *Aaadonta* (Solem, 1976b, p. 473)  
Postapical whorls with major ribs and microsculpture. ....2
2. Shell diameter less than 2.6 mm.; mean whorl count less than 4¼.....3  
Shell diameter more than 2.7 mm.; mean whorl count more than 4½.....5
3. Palatal barriers 4, low ridges (figs. 94e, 95a); Koror and Babelthuap. ....4  
Palatal barriers 5, high blades (fig. 94b); Peleliu. ....  
*Palline notera notera* (p. 229)
4. Palatal barriers 2; Koror.....*Palline notera palauana* (p. 231)  
Palatal barriers 3; Babelthuap. ...*Palline notera gianda* (p. 231)
5. Palatal barriers many (fig. 98b, e).....6  
Palatal barriers 0–1 (fig. 97b).....*Semperdon uncatus* (p. 238)
6. Mean diameter about 4.6 mm.; umbilicus a very narrow slit.....*Semperdon kororensis* (Beddome, 1889) (p. 244)  
Mean diameter 2.9 mm.; umbilicus widely open.....  
*Semperdon xyleborus* (p. 241)



TABLE XI. - SPECIES NUMBERS OF  
ENDODONTOID LAND SNAILS FROM SELECTED GEOGRAPHIC AREAS

	PUNCTIDAE		CHAROPIDAE		ENDODONTIDAE	
	Known	New	Known	New	Known	New
Polynesia, Fiji <sup>1</sup>	1	1	56		143	3
Hawaii <sup>1</sup>	1	?			31	290
Micronesia <sup>1</sup>			29	1	11	
Melanesia <sup>2</sup>			16	4		
New Guinea <sup>3</sup>	1		11			
Indonesia <sup>3</sup>			9			
New Caledonia <sup>4</sup>			49	50(?) <sup>5, 12</sup>		
Lord Howe Id. <sup>6</sup>	8		19			
Norfolk Id. <sup>7</sup>	7		8			
Kermadec Is. <sup>8</sup>	2		7			
New Zealand <sup>9</sup>	80	100+ <sup>17</sup>	147	??		
Australia <sup>10</sup>						
Tasmania	14		38			
Victoria	9		18			
N. S. Wales	3	?	28	8 <sup>11</sup>		
Queensland		4 <sup>11</sup>	14	22 <sup>11</sup>		
S. Australia	4		2			
N. Territory	1		3			
W. Australia	6		10	15 <sup>12</sup>		
Africa <sup>13</sup>	3(?)		114			
St. Helena <sup>14</sup>			11	6		
Neotropica <sup>15</sup> and Juan Fernandez	4(?)		55(?)			
Holarctic <sup>16</sup>	15(?)		2			
TOTALS	159	105	646	106	185	293

<sup>1</sup>Solem (1976b, this monograph, in preparation)<sup>2</sup>Solem (1959a, 1960, 1962, 1963, this monograph)<sup>3</sup>Solem (1958b, 1970a)<sup>4</sup>Solem (1961)<sup>5</sup>Collecting by L. Price and P. Bouchet<sup>6</sup>Iredale (1944) and subsequent collecting<sup>7</sup>Iredale (1945) and subsequent collecting<sup>8</sup>Iredale (1913)<sup>9</sup>Powell (1976)<sup>10</sup>Iredale (1937a, 1937c, 1939)<sup>11</sup>Burch (1976)<sup>12</sup>Collecting by A. Solem<sup>13</sup>Connolly (1939); Solem (1970c)<sup>14</sup>Solem (1978a)<sup>15</sup>Various papers and Odhner (1922)<sup>16</sup>Pilsbry (1948) and various papers<sup>17</sup>F. Climo, personal communication

## SAMOAN ISLANDS

1. Apical whorls with radial ribs.....2
- Apical whorls with spiral cords.....3
2. Aperture without palatal barriers; umbilicus very wide.....3
- Discocharopa aperta* (Möllerndorff, 1888) (p. 76)

Aperture with palatal barriers; umbilicus rather narrow.....  
Endodontidae (Solem, 1976b, p. 126)

3. Aperture with prominent barriers.....4
- Aperture without barriers.....*Sinployea*, see key on p. 119
4. Shell diameter about 3.3 mm.; whorls 4½; Savai'i.....  
    *Graeffedon savaiiensis* (p. 202)
- Shell diameter over 5.0 mm.; whorls about 5; Upolu.....  
    *Graeffedon graeffei* (Mousson, 1869) (p. 200)

## SOCIETY ISLANDS

1. Apical whorls with radial ribs.....2
- Apical whorls with spiral cords.....3
2. Shell diameter less than 2.0 mm.; at most 1 deeply recessed  
    parietal barrier. ....  
    *Discocharopa aperta* (Möllerndorff, 1888) (p. 76)
- Shell diameter over 2.25 mm.; usually several parietal barriers  
    or shell diameter over 3.0 mm. ....  
    Endodontidae (Solem, 1976b, p. 126)
3. Shell minute, diameter less than 1.5 mm.....*Punctum* sp. (p. 57)
- Shell larger, diameter over 2.4 mm.....*Sinployea*, see p. 86

## TONGA

1. Apical whorls with spiral cords predominating, at most low ra-  
    dial swellings. ....2
- Apical whorls with narrow radial ribs.....  
    Endodontidae (Solem, 1976b, p. 126)
2. Aperture without barriers.....3
- Aperture with prominent barriers.....5
3. Diameter less than 3.5 mm.....*Sinployea*, see key on p. 134
- Diameter more than 5.0 mm. ....4
4. Eua; mean diameter about 6.7 mm..*Tuimalila pilsbryi* (p. 179)
- Vavau; mean diameter about 5.7 mm.....  
    *Tuimalila infundibulus* (Hombron & Jacquinot, 1841) (p. 181)
5. Palatal wall bearing a broad ridge (fig. 83b); Eua.....  
    *Vatusila tongensis* (p. 196)
- Palatal wall with 3 barriers (fig. 88e); Tongatapu.....  
    *Graeffedon pricei* (p. 205)

A few species are known from islands that do not fall into the major groups. These species are:

Futuna—*Sinployea vicaria* (Mousson, 1871) (p. 134)

Niue—*Vatusila niueana* (p. 198)

Rotuma—*Sinployea rotumana* (Smith, 1897) (p. 138)

Swains—*Sinployea intermedia* (p. 131)

It must be emphasized that the above keys are adequate for identification of adult specimens in which the sculpture and apertural barriers can be observed. They are less adequate for juveniles and quite inadequate for very worn examples. It still will be possible to collect new species in areas such as the Caroline, Palau, Mariana, Lau, and main Fijian Islands that may or may not key out to a correct genus.

## FAMILY PUNCTIDAE

Generally minute to small endodontoids, primitively with spiral apical sculpture and a combination of macro- and microradial post-apical sculpture that is periostracal in origin. Sculpture altered in larger taxa. Whorl counts and shape highly variable, particularly in New Zealand taxa. Umbilicus open, regularly decoiling to nearly closed. Color monochrome to highly tessellated. A few taxa develop apertural barriers, but most lack barriers. Foot of animal undivided. Prominent pedal and suprapedal grooves unite above tail without forming a caudal foss. Radula with small tricuspid central,

lateromarginals bicuspid with three minute accessory cusps, major cusps becoming reduced in prominence on outer teeth, but not tending to split into additional cusps. Basal plates long and slender, cusps tending to point directly forward. Jaw of separated, square plates, partly fused in larger species. Pallial complex with a bilobed kidney, lobes generally equal in length, primary ureter originating at apex of pericardial kidney lobe, reflexing posteriorly as secondary ureter, opening at ureteric pore alongside to moderately behind the anus and just inside pneumostome. Mantle collar often without lobes or laps, but a glandular extension onto pallial roof present in some taxa. Genital system variable, but apical sections typically as follows: ovotestis of two closely appressed, variously subdivided, teardrop-shaped lobes lying just above stomach apex; hermaphroditic duct a simple, uncoiled tube entering laterally into carrefour swelling; talon with globular head on a short stalk entering apex of carrefour; albumen gland elongate-ovate, deeply indented by loops of intestine and head of spermatheca. Prostate-uterus partly fused to fused, free oviduct short to long, uterus with different glandular zones. Spermatheca with lower shaft expanded, upper shaft more slender after tapering, head ovate, expanded, lying imbedded in base of albumen gland above pallial cavity apex. Vas deferens a slender tube entering penis complex near insertion of penial retractor muscle to well below muscle insertion. Penis complex with a penis-derived epiphallic section in many taxa, interior of penis with long and irregular pilasters, often with a short vergic papilla. Epiphallic section, when present, with slightly different textured pilasters. Entire complex slender and tubelike. Penial retractor muscle arising from diaphragm, inserting on head of penis or epiphallic section, without complexities of insertion. Interior of free oviduct and base of spermathecal shaft with irregular folds in the few examined. Digestive and free muscle systems agreeing with endodontid and charopid patterns. No data are recorded on the nervous system.

The family unit Punctidae is used here in a restricted sense, not as the umbrella for the endodontoids as suggested by Climo (1969a, 1971a, 1978). Pending anatomical confirmation, I include the Punctidae or Punctinae of Northern Hemisphere workers, Laominae in the sense of Suter (1913) and Gabriel (1930), and Paralaomidae of Iredale (1941a, 1944). As a rough estimate, about 159 named taxa from the southern parts of Australia, New Zealand, subantarctic islands, Holarctic, and scattered African localities would be included. Only a very few taxa have had other than jaw and radula data recorded in the literature, and it is quite probable that some of the included species and genera will prove to be charopids and some taxa assigned to the charopids will prove to be punctids. Particularly when shell sculpture becomes reduced, a common pattern in the Austro-Zelandic taxa, assignment to a family group on shell features alone becomes extremely hazardous.

The anatomy of *Punctum* Morse (1864) was illustrated and discussed by Baker (1927, pp. 227–228, pl. 16, figs. 8–12) then reprinted in Pilsbry (1948, pp. 641–643, fig. 349a–f). Data on the shell sculpture formation was given by Solem (1977b, pp. 150–152, figs. 4–6, 11–12). Anatomical data are set forth here on *Punctum* (fig. 24a–b), the New Zealand *Laoma leimonias* (Gray, 1850) (fig. 25a–h), Western Australian *Paralaoma aprica* Iredale, 1939 (fig. 26a–c), and Tasmanian "*Paralaoma*" *coesa* (Legrand, 1871) (fig. 27a–d). These extralimital taxa are illustrated to show the essential unity of structure within the Punctidae and to provide data for comparing charopid patterns.

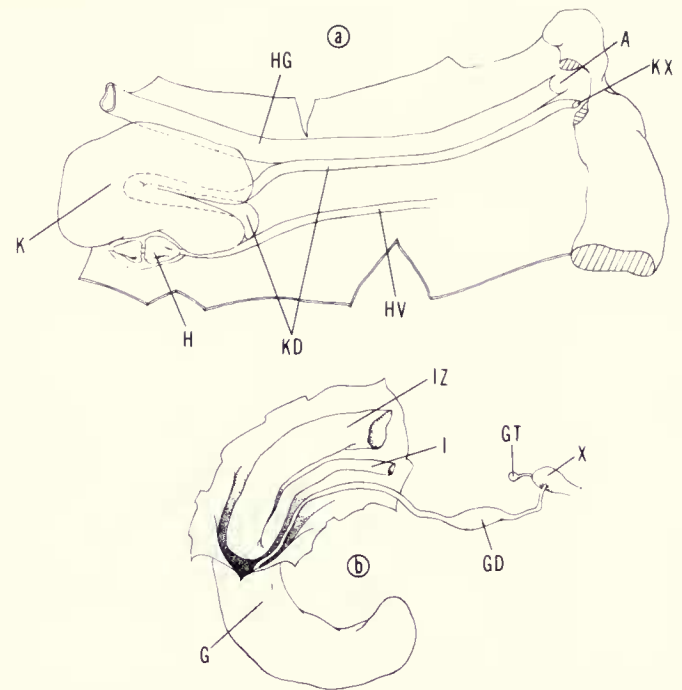


FIG. 24. Partial anatomy of *Punctum minutissimum* (Lea). Cedar bog, Woodburn Road, 4 miles southwest of Urbana, Champaign County, Ohio. E. Kefer! X-20-1969. FMNH 151102: a, pallial region; b, apical genitalia with albumen gland removed. No scale lines prepared. (CW).

To my knowledge, no other taxa have been illustrated in equivalent detail. An anatomical description of *Laoma leimonias* follows to provide detailed comparative data.

#### *Laoma leimonias* (Gray, 1850).

*Description of soft parts.*—Foot and tail slender, rounded posteriorly, not tapering noticeably. Sole undivided, without corrugations (fig. 25d). Pedal grooves high on foot, suprapedal very much smaller than pedal, uniting above tail. Pedal groove passing around tail with a distinct constriction on top of tail. No protruding caudal horn, but top of tail indented, with subpedal region extending posteriorly. No middorsal groove. Slime network very inconspicuous. Body roundly truncated anteriorly.

Body color in preservative yellow white, ommatophores black. Surface of pallial roof and visceral hump with frequent black speckles, less frequent white marks.

Mantle collar (MC) elongated (fig. 25a), with bluntly rounded anterior edge. Basal margin with long intrusion of mantle gland onto pallial roof, corresponding with position of large left anterior mantle lobe (MA) at parietal-palatal angle. Anus (A) opening at inner edge of mantle collar (fig. 25b), slightly anterior to external urinary pore (KX). Urinary chamber (LK) a sharply defined groove that is immediately united with the V-shaped anal channel passing forward in the mantle collar.

Pallial region (fig. 25a–b) very elongated, extending  $1\frac{3}{4}$ –2 whorls apically from aperture. Basal  $\frac{1}{4}$  whorl with glandular extension of mantle collar (MG), longest where major palatal lamella is formed and reabsorbed. Kidney (K) U-shaped, pericardial and rectal branches equal in length. Rectal arm of kidney lapping completely under hindgut (HG) and extending onto parietal margin of pallial cavity (fig. 25c). Thus, rectal arm lies on both parietal and upper palatal margins of pallial cavity. Pericardial arm of kidney appears more slender in Figure 25a, but solely because pericardium lies underneath kidney. Hindgut (HG) paralleling parietal-palatal margin well past apex of pallial region. Loop of intestine (I) with apical base



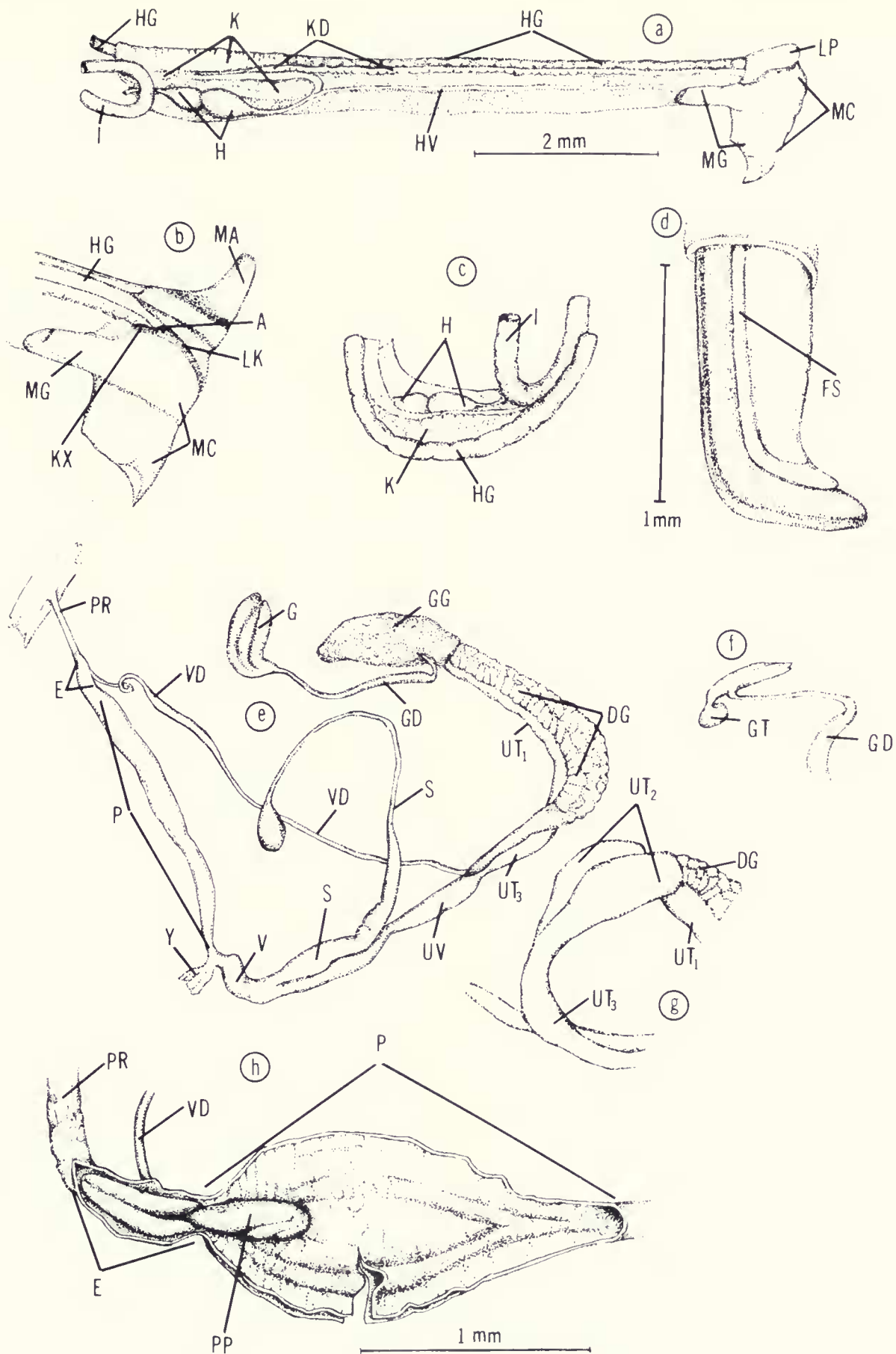


FIG. 25. Anatomy of *Laoma leimonias* (Gray). Herekino Gorge, Kaitaia, Northland, North Island, New Zealand. L. Price! XI-1962. FMNH 135401: a, pallial region; b, detail of pneumostomal openings; c, detail showing extent to which kidney (K) overlaps hindgut (HG); d, extended foot showing pedal grooves and lack of a caudal horn; e, genitalia; f, junction of hermaphroditic duct (GD) and talon (GT); g, detail of uterine structure; h, internal structure of penis and epiphallus. Scale lines as marked. (PS).

of kidney extended above it for a considerable distance. Ureter (KD) sigmurethrous, arms without any lung roof visible between them, not expanded on any portion. When first removed, apical rectal arm of ureter hidden by parietal extension of kidney, but in Figure 25a this is stretched outward. Heart (H) comparatively large, about half as long as kidney, lying partly under pericardial arm of kidney, reaching pallial roof only on basal margin of whorl. Principal pulmonary vein (HV) narrow, reaching mantle gland, without noticeable secondary venation.

Ovotestis (G) composed of 1–2 clumps of finger-like lobes (fig. 25c), buried in apical section of digestive gland above stomach-intestine reflexion, lighter in color than digestive gland. Hermaphroditic duct (GD) slender at first, gradually becoming a thick, lumpy, muscular tube, slightly iridescent in tone. Duct narrows abruptly just at base of albumen gland then reflexes up along albumen gland (GG) before entering duct of talon (GT). Latter a slender tube with expanded head (fig. 25f), entering head of prostate-uterus without differentiated carrefour. Prostate (DG) composed of a few relatively large acini fastened to wall of upper uterine chamber. Lower part of prostate squeezed between uterine sections. Uterus (UT) three-chambered: upper section (UT<sub>1</sub>) a very thin-walled tube, opening into a second chamber (fig. 25g) with glandular walls and two or more low, rounded pilasters (UT<sub>2</sub>). Lower chamber (UT<sub>3</sub>) barely distinguished externally from second chamber, a thin-walled sac with lamellar plates on the wall.

Vas deferens (VD) arising from narrowed base of prostate, a slender tube becoming moderately expanded, then narrowed again before inserting laterally on epiphallus (E) between arms of a narrow U-shaped stimulator (fig. 25h). Vas not tightly bound to penioviducal angle. Epiphallus weakly differentiated from penis, a short swollen tube with a U-shaped stimulator and a narrow neck before joining the penis proper (P). At apex of penis lies a high muscular stimulator (PP), ovate in outline and attached at both ends, its apical tip lying between the arms of the epiphallic stimulator (fig. 25h).

Below penial stimulator, there are two weak "pilasters" caused by folding of the penis wall and very faint spiral pustulations. Basally, penis tapering to a very slender tube before entering short atrium (Y). Gonopore a short slit behind and below right ommatophore.

Free oviduct (UV) long with thick muscular wall, a glandular collar separating its base from spermathecal pore. Spermatheca (S) long, expanded head lying partly in albumen gland and partly in digestive gland, lying above pallial cavity. Lower part of spermathecal stalk slightly larger than oviduct, thin-walled with distinct longitudinal pilasters, narrowing at base of prostate-uterus to a very slender tube, partly buried in acini of prostate. Vagina (V) very short, not differentiated internally from atrium and base of penis.

Buccal mass of average length, high, strongly tapered anteriorly, generative sac small. Buccal retractor massive, not split, inserting at about posterior third of buccal mass in U-shaped fan. Esophagus initially large in diameter, then slender for length of pallial cavity, inserting slightly behind midpoint of buccal mass. Interior of esophagus with weak longitudinal pilasters, becoming fainter apically. Esophagus extends about ¼ whorl past head of pallial cavity, entering stomach along lower parietal margin of shell. Stomach very large, reaching surface of parietal and upper palatal margins, extending apically for slightly more than one whorl. Intestine reflexing along columellar margin to lower margin of kidney base, looping up along kidney base to just below hindgut, reflexing posteriorly and diagonally downward to base of stomach, then looping up to parietal-palatal margin and running forward as hindgut. Hindgut follows parietal-palatal margin along edge of pallial cavity to anus. Loop of intestine abutting kidney projects into kidney, which extends outside of intestine apically, thus separating body wall from pallial roof.

Salivary glands white, lying alongside esophagus, touching medially, near posterior end. Salivary ducts straight, entering laterally on base of esophagus.

Digestive gland extending from apex of soft parts to apex of pallial cavity, reduced in region of stomach, distinctly darker in color than ovotestis.

Free muscle system simple: buccal retractor massive, not split anteriorly, uniting with tail fan to form columellar retractor about two whorls above aperture. Right ommatophoral retractor passing between penioviducal angle. Rhinophoral retractors very short, uniting with ommatophorals just before union with tail fan. Entire free muscle system short and massive, extending apically less than 2½ whorls from aperture.

(Based on 4 adult examples from south side of Herekino Gorge, 10 mi. southwest of Kaitaia, Northland, New Zealand (35° 17' S, 173° 12' E), FMNH 135401. Collected by L. Price, November 1962.)

Of the dissected species, *Punctum minutissimum* (Lea, 1841) and *Paralaoma aprica* (Iredale, 1939) are in the 1.5–2.0 mm. size range; *Laoma leimonias* (Gray, 1850) is a very high-spined shell, about 2.3 mm. in diameter and 2.7 mm. high with 7 whorls; and "*Paralaoma*" *coesa* (Legrand, 1871) is the largest species, about 3.5–4.0 mm. in diameter, with 4½ whorls. As a systematic comment, *Punctum* and *Paralaoma* may well be synonyms, but "*Paralaoma*" *coesa* probably does not belong to the same genus. There are nomenclatural problems in dealing with this species. The very long, free oviduct and penis of *Laoma* is related to the greatly increased whorl count of that species and has no special systematic significance.

The basic anatomical features of the Punctidae are: (1) the bicuspid lateromarginal teeth with minute accessory cusps (fig. 12b–e), long basal plates, and forward pointing of the rounded cusps; (2) the ovotestis of two teardrop-shaped lobes that may be appressed (figs. 24b, 25e, 26c) or modestly separated (fig. 27b) and are subdivided to various extents (compare figs. 24b and 27b with Baker, 1927, p. 16, fig. 8); (3) the bilobed kidney of approximately equal lobe length, with (fig. 27a) or without (figs. 24a, 25a, 26a) lung roof visible between the ureter arms; (4) the slender penis complex with simple insertion of the penial retractor muscle that internally has a penis-derived epiphallic section followed by vergic papilla and smooth regular to irregular pilasters; and (5) normally rather slender terminal female genitalia with tapering lower spermathecal stalk, internally with free oviduct, vagina, and spermatheca sharing smooth pilaster sculpture.

The Charopidae contrast in having: (1) tricuspid laterals and marginals with rectangular basal plates, a simplified interrow tooth support system during feeding, and upward-slanting pointed cusps (figs. 13–14); (2) the ovotestis consisting of one to two clumps of several long follicles that lie parallel to the shell axis (figs. 90i, 100b–c, g); (3) a generally bilobed kidney in which the lobes may be equal in length (figs. 39c, 90a), the rectal much longer (figs. 53a, e, 90e), or infrequently the pericardial lobe is longer (fig. 11a), and there may (fig. 39c) or may not (fig. 90e) be lung roof visible between the arms of the ureter; (4) the penis complex normally is short and fat (fig. 90b, f, i), with simple to complex insertion of the penial retractor muscle, the penis frequently with a verge, complex stimulators and stimulator pockets, a vas deferens-derived epiphallus in many taxa, and the lower penis area without sculpture; and (5) normally thick terminal female



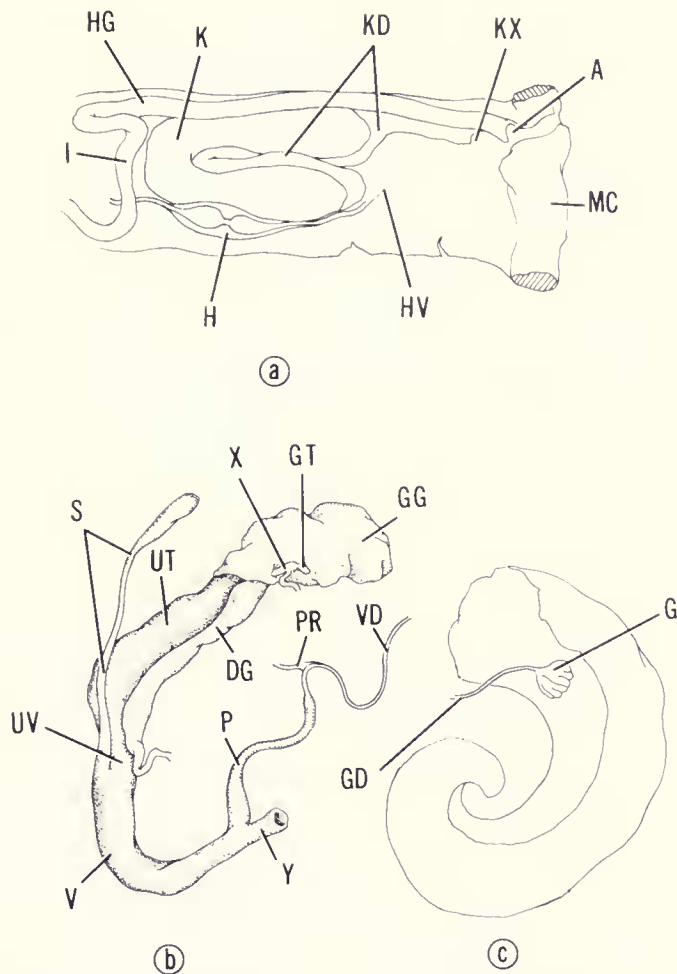


FIG. 26. Partial anatomy of *Paralaoma aprica* Iredale. Station WA-98, north end of townsite reserve, Nangeenan, west of Merredin, Western Australia. A. Solem and L. Price! II-22-1974. FMNH 182222: a, pallial region; b, postapical genitalia; c, apical genitalia. Scale lines as marked. (EL).

genitalia with very thick spermathecal base that rather abruptly narrows to the mid stalk, internally often with very prominent pilasters that may be corrugated (fig. 9d) or smooth but very sharply defined (fig. 87c).

The Endodontidae contrast to both in having: (1) bicuspid laterals and marginals with the marginal ectocones split (Solem, 1976b, p. 91, fig. 54a–f), rectangular basal plates with interrow support system (Solem, 1976b, p. 89, fig. 52d), and rather sharp elevation of the pointed cusps (Solem, 1976b, p. 89, fig. 52b); (2) the ovotestis of multiple clumps angled to the shell axis (Solem, 1976b, p. 372, fig. 163c); (3) the kidney with at most a weak rectal lobe developed and only a primary ureter that opens at the front edge of the rectal kidney lobe near the posterior of the pallial cavity (Solem, 1976b, p. 459, fig. 195a); (4) a slender penis that normally has only two simple longitudinal pilasters, never a verge or vergic papilla, only rarely a penis chamber-derived epiphallic section (Solem, 1976b, p. 396, fig. 171b–c, h); and (5) very thin terminal female genitalia without special internal sculpture and with highly var-

iable insertion of the spermathecal stalk (Solem, 1976b, p. 84, fig. 48a–c). In addition, the complete separation of the prostate and uterus and apparent absence of a sperm packet in the Endodontidae are major differences from either of the other families.

The changes outlined above are noncorrelated, and their different states in the three families indicate that the families represent three separate patterns of diversification. These differences are greater than those seen between limacacean families and thus merit recognition as family units. Whether the punctid radula is correlated with specialized feeding habits as opposed to those of the Charopidae and Endodontidae is unknown.

The Punctidae are only marginally present in the Pacific Island area, with a scattering of records in Hawaii, a single record from the mountains of Tahiti, and a new species, *Punctum polynesticum*, described here from the Austral Islands. Thus, no attempt is made at revising the generic classification or discussing detailed patterns of distribution. Reference of these Pacific specimens to *Punctum* is based strictly on conchological similarity in the absence of preserved specimens. The distinction between *Paralaoma* and *Punctum* may not be maintained in the future, but the shells of the Pacific Island taxa are far more similar to the Holarctic *Punctum* than to the Austro-Zelandic *Paralaoma*. In view of the limited material, no diagnosis is presented of the genus *Punctum*.

#### Genus *Punctum* Morse, 1864

*Type species*.—*Helix minutissima* Lea, 1841, by original designation.

There are about 50 sets of *Punctum* from various Hawaiian Islands in the Bernice P. Bishop Museum which may be lumped temporarily as *Punctum horneri* Ancy (1904, p. 66, pl. 5, figs. 11–12), but no material has been reported previously from Polynesia. A single specimen (BPBM 145298) from Station 865, Mt. Aorai Trail, Tahiti, collected between 5,600 and 6,300 ft. elevation, can be identified as a *Punctum*, but is too fragmentary for any attempt at giving it a specific name. The high spire and narrow umbilicus of the fragment combine with the finer and less protracted sculpture to place it in *Punctum* rather than *Striatura*.

*Euconulus* (*Monoconulus*) *conoidea* H. B. Baker (1941, pp. 214–215), the only non-Hawaiian Pacific Island *Euconulus* known to date, was taken at the same collecting station. Presence of these otherwise Hawaiian and Holarctic taxa in Tahiti at high elevations could be explained by the *deus ex machina* of accidental transport on the feathers of migratory birds.

More abundant material of quite different species from the Austral Islands is described below as *Punctum polynesticum*. Although somewhat atypical in whorl count and heavy sculpture, it is nearer to *Punctum* than any other genus known to me. Only dead specimens were available. Measurements are summarized in Table XII.

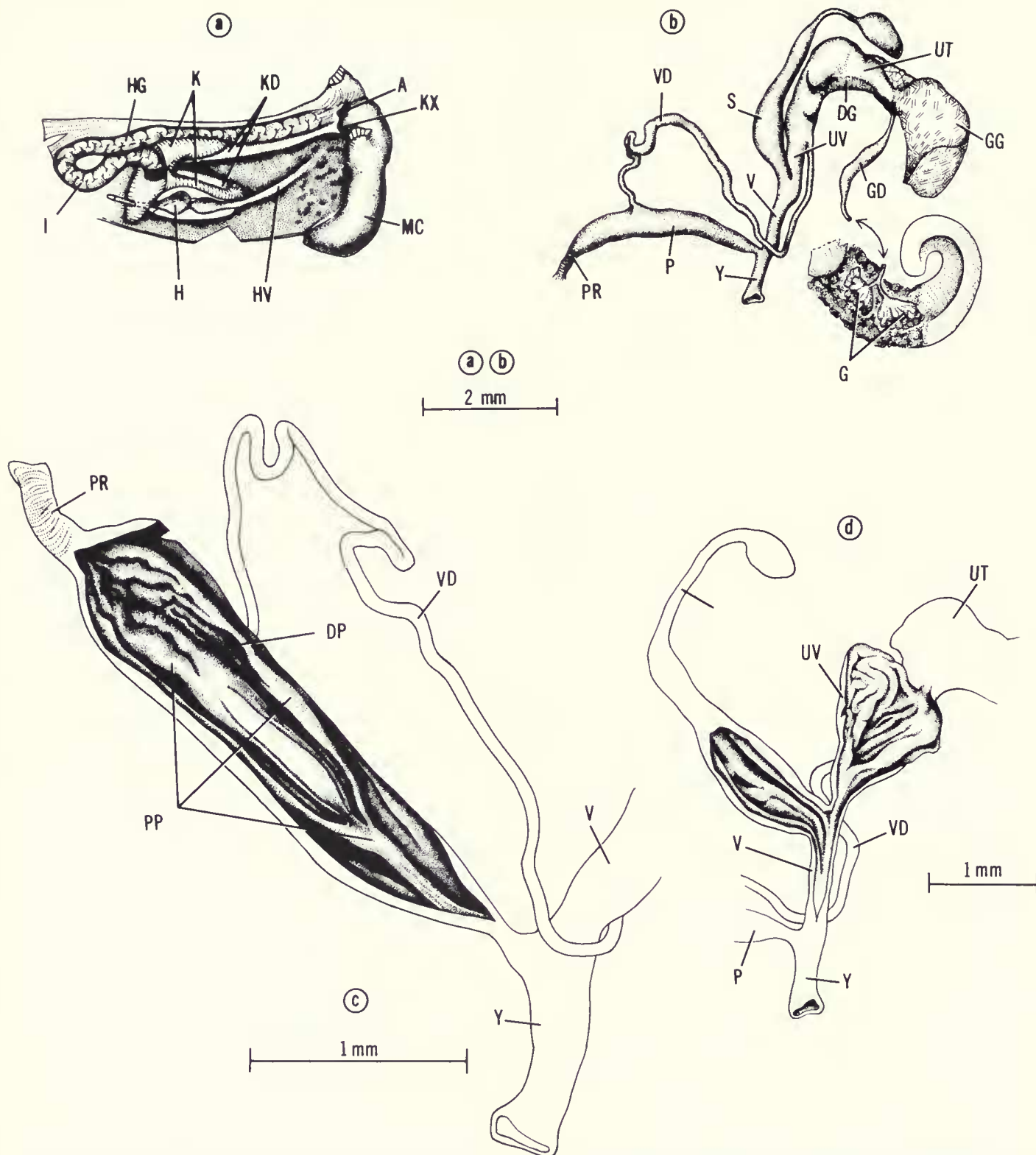


FIG. 27. Anatomy of "*Paralaoma*" *coesa* (Legrand). Station TA-38, Circular Head, near Stanley, North Tasmania. L. Price! XI-8-1966. FMNH 154974: a, pallial region; b, genitalia; c, interior of penis; d, interior of free oviduct and spermatheca. Scale lines as marked. (NB).

### *Punctum polynesianum*, new species. Figure 28a-c.

**Diagnosis.**—Shell minute, diameter 0.95–1.02 mm. (mean 0.99 mm.), with  $3\frac{3}{4}$ – $3\frac{3}{4}$ + rather tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending more rapidly, spire protrusion about  $\frac{1}{4}$  body whorl width (0.30–0.34 mm.), H/D ratio 0.563–0.597 (mean 0.580). Apical whorls  $1\frac{1}{2}$ , sculpture of about 15 fine spiral cords, whose interstices are 3–4 times their

width. Postnuclear whorls with narrow, rounded, strongly protractively sinuated, prominent radial ribs, 72–83 (mean 77.3) on the body whorl, whose interstices are about twice their width until end of body whorl where ribbing becomes crowded. Ribs/mm. 23.2–25.9 (mean 24.9). Microsculpture of fine radial riblets, 2–3 between each pair of major ribs, crossed by equally fine spiral riblets. Umbilicus shallow, broadly V-shaped, regularly decoiling, contained 3.33–3.44 times (mean 3.37) in the diameter, margins rounded. Sutures deep,



TABLE XII. — RANGE OF VARIATION IN PUNCTUM, DISCOCHAROPA, AND MICROCHAROPA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>Punctum</u>						
<u>polynesianum</u>	6	77.3(72-83)	24.9(23.2-25.9)	0.58(0.56-0.61)	0.99(0.95-1.02)	0.580(0.563-0.597)
<u>Discocharopa</u>						
<u>aperta</u> (MlIdf.)	310	110.6(77-148)	26.9(18.0-40.4)	0.59(0.48-0.74)	1.36(1.18-1.84)	0.438(0.341-0.615)
<u>Microcharopa</u>						
<u>mimula</u>	30	126.6(117-136)	36.5(32.3-40.5)	0.48(0.43-0.53)	1.07(0.95-1.13)	0.449(0.400-0.469)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BW
<u>polyn.</u>	3 1/4(3 1/8-3 3/8)	0.29(0.28-0.30)	3.37(3.33-3.44)	Circa 15	0.08(0.07-0.10)	0.32(0.30-0.34)	0.255(0.216-0.316)
<u>aperta</u>	3 1/2-(3 1/8-4 1/4)	0.54(0.43-0.92)	2.58(2.00-3.21)	MAJOR RADIALS	0.07(0.03-0.15)	0.40(0.35-0.44)	0.170(0.086-0.286)
<u>mimula</u>	3 1/4-(3 1/8-3 3/8)	0.40(0.35-0.46)	2.68(2.43-3.05)	17.8(16-20)	0.05(0.04-0.07)	0.32(0.28-0.34)	0.186(0.118-0.289)

whorls strongly rounded, with slight lateral compression above periphery and on basal margin. Aperture circular, inclined about 30° from shell axis. Color light yellow-horn, without darker markings.

*Punctum polynesianum* is the smallest species yet described within the genus. Its very prominent radial ribbing and rather wide umbilicus separate it from most species. *Punctum vitreum* H. B. Baker, 1930, is perhaps nearest in strength of ribbing, but is a much larger shell with a lower H/D ratio.

*Description.*—Shell minute, with slightly more than 3¼ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending much more rapidly, H/D ratio 0.589. Apical whorls 1¼, sculpture partly eroded. Postnuclear sculpture and microsculpture as in diagnosis, 83 ribs on the body whorl. Umbilicus broadly V-shaped, regularly decoiling, contained 3.35 times in the diameter. Sutures and whorl contour typical, aperture shape and inclination as in diagnosis. Height of holotype 0.59 mm., diameter 1.02 mm.

*Holotype.*—Austral Islands: Raivavae, Station 622, Ahuovi Point. Collected dead under *hau* leaves by Y. Kondo, D. Anderson, and C. M. Cooke, Jr., on August 9, 1934. BPBM 147099.

*Range.*—Tubuai and Raivavae, Austral Islands.

*Paratypes.*—Raivavae: west side Vaiaunana Peninsula (Station 587), 100 yd. inland at 200 ft. elevation, under dead leaves (three specimens, BPBM 146725). Tubuai: southwest of Murivai (Station 698), 300-400 yd. inland under *Barringtonia* trees (two specimens, BPBM 147679).

*Remarks.*—Without preserved material for dissection, classification of this species will remain uncertain. The presence of endodontoid reticulated microsculpture between the major ribs, rather than the transverse growth wrinkles seen in *Striatura* (Solem, 1977b, p. 151, fig. 1) has dictated my placing this species in *Punctum*. In several respects *P. polynesianum* agrees more with *Striatura*. The latter averages fewer whorls (3¼-3½) and has a wider umbilicus than does *Punctum* with its 3¾-4¼ whorls and generally narrower umbilicus. Apical sculpture in *Striatura* is generally more prominent and narrower, whereas in *Punctum* it is wider and lower. The low whorl count

and fine apical sculpture of *P. polynesianum* thus appear somewhat anomalous.

Neither genus has been reported from South Pacific Islands, although both live in Hawaii. A typically sculptured *Punctum* is reported from Tahiti above, but this species is very different in form, color, shell thickness, and ribbing from *P. polynesianum*. *Microcharopa* could be confused on the basis of size, but that species has radically different apical sculpture (see fig. 4, p. 13), a much lower H/D ratio (mean 0.449), and many more, much finer radial ribs (117-136 on the body whorl).

An alternative possibility is that this species represents the outermost Polynesian representative of the Charopidae and is related to *Sinployea*. I consider it much more probable that it is a *Punctum* accidentally introduced by migratory birds. In the absence of dissections, no subgeneric reference would be meaningful.

## FAMILY CHAROPIDAE

Small to large endodontoids, apical sculpture of shell very diverse, postapical whorls primitively with major radial ribs and a microsculpture of radial riblets and secondary spiral elements, most sculpture features composed of periostracal elements only. Many taxa with sculpture secondarily reduced to lost. Whorl counts and shell shape highly variable. Umbilicus widely open to closed. Color monochrome to brightly tessellated. Apertural barriers evolved independently in several lineages, most species without trace of barriers. Visceral hump and shell greatly reduced to almost lost in a few taxa. Foot of animal undivided, prominent pedal and suprapedal grooves uniting above tail, in some taxa forming a caudal foss or mucus pore. Radula with tricuspid central slightly to distinctly smaller than normally tricuspid laterals, rarely bicuspid or with only one cusp. Marginals frequently tricuspid, sometimes with ectoconal splitting. Basal plates of central and marginal teeth rectangular, interrow support system well developed, latter absent on marginals. Cusps of major teeth sharp and tending to point upward with ectocones elevated much more than in Endodontidae. Jaw of separated, squarish plates in smaller species, becoming partly to completely fused in larger taxa. Pallial complex usually with a distinctly bilobed kidney, relative size of lobes quite variable among species, plus a closed secondary ureter that normally opens just inside pneumostome. Some taxa with only a partial secondary ureter that opens far

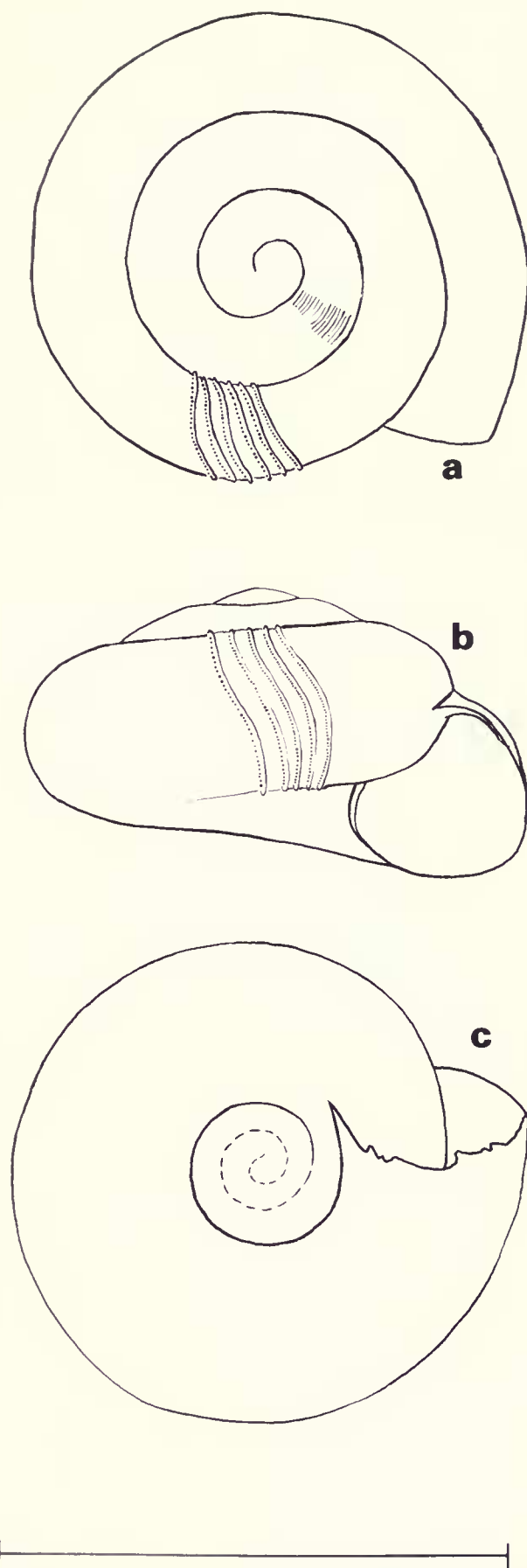


FIG. 28. a-c, *Punctum polynesianum*, new species. Station 622, Ahuovi Point, Raivavae, Austral Islands. Holotype. BPBM 147099. Scale line equals 1 mm. (LH).

posteriorly in the pallial cavity, and/or rectal kidney lobe greatly reduced. Mantle collar normally without prominent lobes or laps, a glandular extension onto pallial roof found in some taxa. Genital system highly variable. Ovotestis typically of one or two clumps of long follicles that lie parallel to the outer wall of the body cavity and occur sequentially. Some taxa with the ovotestis broken up into a series of lobes that are perpendicular to the outer wall of the body cavity and widely separated from each other, a few taxa with follicles shortened and resembling those of the Punctidae. Hermaphroditic duct a simple unkinked, usually iridescent tube entering usually laterally onto apex of carrefour. Talon a finger-like projection or swollen head on a short stalk. Albumen gland irregular in shape, deeply indented by loops of intestine and head of spermatheca. Prostate and uterus fused with partial common lumen, uterus with separate and sequential glandular sections. Free oviduct short to long, thin, base of spermatheca and upper vagina normally swollen. Spermathecal shaft tapering abruptly, head above apex of pallial cavity, an expanded oval, to elongate oval structure. Vas deferens slender, normally entering a clearly differentiated epiphallus, often through a complex valvular pore. Many taxa with epiphallus secondarily compressed into penis or absent. Penis usually fat, at least in upper section, not usually long and slender, lower part often a thin tube. Interior of penis frequently with a well-developed verge, circular ridges, stimulatory pilasters, and pocket stimulators. Penis retractor arising from diaphragm, usually very short, inserting in simple to complex fashion on the penis or epiphallus. Interior of lower female tract simple to with very large longitudinal simple to corrugated pilasters, openings to free oviduct and/or spermathecal shaft varying from simple pores to with complex valves. Penis, so far as observed, enervated from right cerebral ganglion. Digestive and free muscle system typically endodontoid.

The Charopidae, as rather broadly defined here, includes the Phenacohelcidae, Otoconchinae, Flamulinidae, Rotadiscinae, Amphidoxinae, Dipnelicidae, Hedleyoconchidae, and Pseudocharopidae of authors. In terms of species, it is the dominant land snail group of New Zealand (Powell, 1976; Climo, 1969a-b, 1970, 1971a-b, 1978), New Caledonia (Franc, 1957; Solem, 1961), parts of Australia (Tasmania, Victoria, less abundant in New South Wales, South Australia, southwestern Western Australia, sparse in the Northern Territory, well represented in the rain forest areas of Queensland; Iredale, 1937a-c, 1939, 1941a-b; Burch, 1976; Solem, in preparation C), Lord Howe Island (Iredale, 1944), Norfolk Island (Iredale, 1945), and Kermadec Islands (Iredale, 1913). The Charopidae is only sparsely represented in Indonesia (Solem, 1958), New Guinea (Solem, 1958, 1959b, 1970a), Solomon Islands (Solem, 1960), and New Hebrides (Solem, 1959a). Charopids occur with varying abundance on the islands surveyed in this report.

Extralimital to the Pacific Basin, species of charopids are common to dominant in southern Africa (Connolly, 1939; Solem, 1970c), were common on St. Helena (Solem, 1977c), and *Notodiscus* (Solem, 1968c) is found on the Subantarctic Islands (Kerguelen, Possession, Heard, Marion, Amsterdam). There is a modest Juan Fernandez radiation (Ohdner, 1922) and many scattered descriptions and records from southern South America, the Andes, and Central America. Two species occur in western North America as far north as Idaho and Montana (Pilsbry, 1948).

Including the taxa discussed and described below, approximately 646 named species are included in the



Charopidae. This is a very conservative estimate of actual extant diversity because Climo (personal communication) has large numbers of undescribed New Zealand taxa, a rain forest patch survey of Queensland and Northern New South Wales revealed approximately 30 undescribed taxa (Burch, 1976), and my own 1974 and 1976–1977 field collections in southwestern Western Australia produced at least 15 new species (Solem, in preparation C). In contrast, several years of intensive fieldwork in Victoria by Brian Smith and associates from the National Museum of Victoria have confirmed the described diversity and greatly extended ranges but have not produced new taxa. It is thus impossible to present an accurate estimate of diversity in the Charopidae at the present time, except to state that the currently recorded taxa are significantly less in number than the extant taxa.

A breakdown on estimated endodontoid species numbers is given in Table XI. The grand total of 1,494 described and collected but undescribed taxa contrasts with the species estimate given by Boss (1971, p. 108) of only 502 species of endodontoid land snails. A critique of Boss's assumptions and procedures was included in Solem (1978b).

Because this monograph deals with taxa from only one area of species abundance, it is inappropriate to try for a worldwide revision of higher categories. More important, data in the literature is not adequate to make higher level taxonomic decisions, and only part of the material needed to work out these problems is available, dissected, and illustrated. Illustrations and descriptions needed to justify most synonymization of family names and to emphasize the broad distributions involved are published, but work on the Western Australian taxa (Solem, in preparation C), including the Dipnelicidae, is omitted at this time.

Where possible, actual type species have been dissected and illustrated, but in taxa such as *Paralaoma* (figs. 26–27) this was not possible. Anatomical illustrations and descriptions of *Charopa coma* (Gray, 1843) (figs. 9–10), *Phenacohelix pilula* (Reeve, 1852) (fig. 11), *Flammulina zebra* (Le Guillou, 1842) (fig. 29), *Amphidoxa marmorella* (Pfeiffer, 1845) (fig. 30), *Stephanoda binneyana* (Pfeiffer, 1847) (fig. 31), and *Pseudocharopa lidgbirdi* (Etheridge, 1889) (fig. 32), based on new dissections, are presented here. Literature data on the anatomy of *Rotadiscus* (Baker, 1927, pp. 228–230, pl. 16, figs. 13–20) and the Otoconchinae (Climo, 1969a, fig. 2C; 1971a) allow handling of all the included subfamily names except the Hedleyoconchinae. This Australian group, fairly common in New South Wales and Queensland, with a possible relative on Lord Howe Island (Iredale, 1944, pp. 317–318), has not been dissected, but probably is another example of shell sculpture reduction and spire elevation in an arboreal taxon. External body features, jaw, and radula were figured by Hedley (1888, fig.; 1889, pl. 15) and copied by Pilsbry (1893–1895, pl. 9, figs. 27–29). These features are typically charopid in aspect.

Australian and New Zealand workers have variously used the names Flammulinidae, Charopidae, Phenacohelicidae, and Otoconchidae for subgroups of this complex (Gabriel, 1930; Iredale, 1937a *et seq.*; Climo, 1969a–b, 1970, 1971a–b, 1978; Powell, 1976). In large part this was based on early work of Henry Suter, which was summarized in his magnificent monograph (Suter, 1913). The ancient question as to the significance of the caudal pore or foss was discussed above and well summarized by Climo (1969a). It has no major taxonomic utility. Climo (1969a) focused on the presence or absence of an epiphallus as a significant subfamily key character. The externally easily recognizable epiphallus of *Charopa* (fig. 9b, d) does contrast with the situation in *Phenacohelix* (fig. 11c, e) where the insertion of the penial retractor has shifted to the epiphallus-vas deferens junction, rather than inserting on the penis-epiphallus junction as in *Charopa*. In *Flammulina* (fig. 29b, e–j) the situation is complicated by visceral hump reduction and drastic increase in whorl profile cross-sectional area. In *Flammulina zebra*, the genotype, the epiphallus has been compacted back into the penis (fig. 29e–h) and is thus completely undetectable from external view (fig. 29b). In other taxa referred to *Flammulina* (Climo, 1969a, fig. 2A) and the Otoconchinae (Climo, 1969a, fig. 2B–C; 1971a, fig. 1E–F) greater compaction has taken place in the region of the prostate and uterus, whereas the penis and epiphallus region are maintained as separate entities.

Anatomical descriptions of the family units' type genera follow to provide comparative data with the later dissections and to record structural variations for consideration by future revisors of extralimital taxa. The descriptions follow the same sequence as the illustrations—*Charopa coma* (Gray) (figs. 9–10), *Phenacohelix pilula* (Reeve) (fig. 11), *Flammulina zebra* (Le Guillou) (fig. 29), *Amphidoxa marmorella* (Pfeiffer) (fig. 30), *Stephanoda binneyana* (Pfeiffer) (fig. 31), and illustrations only of *Pseudocharopa lidgbirdi* (Etheridge) (fig. 32). Discussion of anatomical variation in that species is deferred to a review of the patterns in Lord Howe Island taxa (Solem, in preparation). Nomenclatural details and a shell description of *Amphidoxa marmorella* are included because so little has been recorded about this species.

#### **Charopa coma** (Gray, 1843).

*Description of soft parts.*—Foot and tail slender, rounded posteriorly, but not tapering. Sole undivided and without any corrugations (fig. 9a). Pedal grooves not particularly high on foot, suprapedal less distinct than pedal, both grooves uniting over tail. No caudal horn or foss. Middorsal groove weak. Slime network rectangular, fairly inconspicuous. Head extended well in front of foot, which is squarely truncated anteriorly. Ommatophores long.

Body color in preservative light yellow-white, ommatophores black.

Mantle collar (MC) rather narrow (fig. 9e–f) with a large glandular extension (MG) encroaching on lung surface. Pneumostome (LP) masked by quite small left anterior mantle lobe (MA) at parietal-palatal angle. Anus (A) opening slightly anterior to external ureteric

pore (KX) and sharing single opening with pneumostome (LP). Urinary chamber (LK) a narrow groove angling past anus.

Pallial region (fig. 9e) varying in length from  $\frac{3}{4}$ –1 whorl, elongated, anterior portion filled with mantle gland (MG). Lung roof clear, except for occasional white speckles near kidney tip. Kidney (K) U-shaped, rectal arm equal in length to pericardial, but distinctly more slender, lapping under hindgut. Hindgut (HG) paralleling parietal-palatal margin past top of pallial cavity, slender. Kidney abutting on loop of intestine (I). Ureter (KD) sigmurethrous, not expanded at any portion, both arms compressed between lobes of kidney, then bordering hindgut to external ureteric opening (KX). Heart (H) proportionately large, much shorter than kidney. Principal pulmonary vein following edge of kidney, then running forward to edge of mantle gland. No conspicuous secondary venation.

Ovotestis (G) embedded in apical lobe of liver (fig. 9b), variable in form and spacing, consisting of a few finger-like lobes, often split one or more times. Individual lobes with slender pink rods. Mass of ovotestis may be concentrated at one point or divided into two masses separated by part of digestive gland. Hermaphroditic duct (GD) straight, thick-walled, iridescent pink, sometimes with one or more knobs on surface, narrowing slightly to radically just before reaching albumen gland (GG) and entering midway on talon (fig. 9b, GT). Latter a blind pouch buried in albumen gland, head enlarged and pink, duct slender, passing straight into head of prostate-uterus. Prostate (DG) of large rectangular glandular lobes pressed against surface of uterine sector. Uterus (UT) an extremely thin-walled circular tube partly filled with spongy tissue opening through a constricted collar into a thick-walled, white, expanded glandular pore with smooth inner walls except for a single large pilaster. Muscle fibers pass from uterine base to columellar retractor.

Vas deferens (VD) arising from narrowing of prostate along glandular section of uterus, first part expanded, then continuing as narrow tube along free oviduct and vagina to penioviducal angle, then up penis to epiphallus (E). Epiphallus short, thick-walled, expanded, internally (fig. 10) with two longitudinal pilasters, reflexed and entering penis (P) through a small verge (fig. 9d, PV). Penial retractor muscle (PR) arising on diaphragm, attached to apex of penis in a U-shaped fan. Penis expanded, internally with thick pustulose glandular lining extending from apex to near base which terminates in a thickened collar. Verge small, with terminal pore, not developed in juveniles. Below level of verge, a blind pocket with smoothly muscled walls develops. This "penial caecum" (PC) is strictly internal and not visible on outside of penis. Glandular collar considerably thicker than rest of penis interior and gives false appearance of being a verge when atrium (Y) opened.

Length of free oviduct (UV) highly variable, apparently correlated with length of pallial region. In figured individual it is extremely short; in others almost equal to vagina in length. Base of free oviduct constricted by a glandular papilla with central pore (UVO). Spermatheca (S) with very slender duct, bound to surface of prostate, passing into visceral mass above pallial cavity and expanding into a distinct head. Albumen gland also in mass of digestive gland and intestinal loop above pallial cavity. Vagina (V) long, swollen medially, with a prominent tubercle, or set of tubercles (VS), located between oviducal pore and the several longitudinal pilasters that extend to atrium (Y). Latter short, thin-walled, opening into gonopore, a transverse slit located just behind and above right rhinophore.

Free muscle system simple. Tentacular retractors (TP) uniting with tail fan (FR) well in front of union with buccal retractor (BR). Point of union between ommatophoral (TER) and rhinophoral (TVR) retractors variable, usually about midway along distance to tail fan. Right ommatophoral retractor passing between penioviducal angle.

Buccal mass (B) short and high (fig. 9g), with very slender generative sac. Buccal retractors (BR) insert as U-shaped fan about  $\frac{1}{4}$  of way from posterior end. Esophagus (BE) very long and slender, originating high on buccal mass only slightly behind midpoint and well in front of buccal retractor insertion. Interior of esophagus with longitudinal ribs. Stomach originating just above pallial cavity, extending apically for  $\frac{3}{4}$  of a whorl and with reflexion of stomach at point well below first lobe of ovotestis. First arm of intestine follow-

ing lower inner margin of whorl to base of kidney, looping below cephalic aorta and across base of kidney, then reflexing for less than  $\frac{1}{6}$  length of stomach, rising to upper parietal-palatal margin and passing forward as hindgut.

Digestive gland extending from apex of soft parts to just above intestinal loop, lower parts finger-like because of the huge stomach. Main artery, granular white in color, empties primarily into stomach and secondarily into recurved lower loop of intestine.

Salivary glands (OG) elongate, situated on sides and top of esophagus, closely associated with prostate-uterus in body cavity. Salivary ducts (OD) straight, inserting on each side at base of esophagus.

(Based on FMNH 135420, Waiwera-Puhoi Road, North of Auckland, North Island, New Zealand, A. Solem! February 10, 1962. Several adults and juveniles.)

### **Phenacohelix pilula (Reeve, 1852).**

*Description of soft parts.*—Foot long and slender, tapering gradually to a sharply rounded posterior margin. Sole undivided, without corrugations. Pedal grooves very high on foot, suprapedal distinctly less impressed than pedal, both grooves uniting over tail. Caudal horn a very long, tapering projection (fig. 11b, CH). Middorsal groove absent. Slime network very weak, barely visible. Head extending only slightly in front of foot, which is bluntly rounded anteriorly.

Body color in preservative yellow-white, with faint grayish tinge to upper part of tail and caudal horn, ommatophores reddish black. Dark color markings on pallial roof visible through shell.

Mantle collar (MC) narrow (fig. 11a), with moderate glandular intrusion (MG) onto pallial roof. Pneumostome without clearly defined lappets. Anus (A) opening above and slightly anterior to external ureteric pore (KX), urinary chamber (LK) a shallow groove leading past anus and fading out toward mantle collar margin.

Pallial region (fig. 11a) rather short and compact. Lung roof with numerous scattered black speckles and much less frequent white patches. Kidney (K) bilobed, pericardial arm much longer than rectal, 3.5 times length of pericardium (H). Base of kidney abutting on loop of intestine. Rectal arm of kidney lapping under hindgut, less than half length of pericardial arm. Ureter (KD) sigmurethrous, pericardial arm slightly expanded over that along hindgut (HG). A clear section of lung roof visible between arms of ureter. Neither ureter nor hindgut expanded during anterior passage toward pneumostome. Hindgut (HG) paralleling parietal-palatal angle well past apex of pallial cavity. Heart (H) short, angled to plane of hindgut. Principal pulmonary vein (HV) simple, extending forward to edge of mantle gland intrusion, without conspicuous secondary venation.

Ovotestis (fig. 11c, G) buried in apical lobes of digestive gland above stomach-intestine reflexion, consisting of one or two clumps of pinkish iridescent finger-like alveoli joined by slender ducts in a "Y" leading to main hermaphroditic duct (GD). Latter a slender duct tapering gradually toward an enormously swollen portion, about  $\frac{1}{4}$  of duct length, shortly before an approach to albumen gland, then becoming an extremely slender tube before joining talon (fig. 11d, GT), which is buried in albumen gland (GG). Latter a blunt, finger-like projection lying buried in visceral hump above pallial cavity and composed of quite large acini with a yellow-orange tinge. Basal portion of hermaphroditic duct reaching base of albumen gland, reflexed apically along surface before entering laterally upon enlarged head of talon, which is partly buried within albumen gland. Narrowed shaft of talon running to head of prostate-uterus, no expanded carrefour visible. Prostate (GD) of much larger, lighter colored acini than those of albumen gland, fastening to thin-walled, upper uterine chamber. This is a flat, smooth tube gradually tapering from a narrow apex to a broad base where the second uterine chamber (UT<sub>2</sub>), a glandular walled structure, expands. Lower part of uterus a thin-walled chamber with internal lamellar plates, opening into a bulbously expanded free oviduct.

Vas deferens (VD) arising as groove from base of prostate, partly hidden by third uterine chamber, passing down as a thin-walled tube



to penioviducal angle (to which it is lightly bound by fibers), reflexing along penis and becoming progressively larger in diameter and more muscular before joining epiphallus laterally. Penial retractor (PR) inserting directly on head of epiphallus (E), a short, solid, globose tissue mass arising on diaphragm. Epiphallus an expanded muscular tube entering penis (P) through a smooth muscular verge (fig. 11e, PV). Walls of penis with weak crenulated pilasters and pustulations basally, apical portion with glandular collar just below tip of verge. Externally, position of glandular collar and verge indicated by swelling in penis-epiphallus. Atrium (Y) shortened and leading to gonopore located below and a little behind right ommatophore.

Free oviduct (UV) a short, globosely expanded structure narrowing slightly to point of union with spermathecal stalk. Spermatheca (S) with very slender stalk, partly buried between acini of prostate, passing apically to small expanded head lying above apex of pallial cavity in visceral mass together with albumen gland and talon. Vagina (V) much longer than free oviduct with a very thin-walled accessory pocket that was badly torn in all dissected specimens. The exact relationship of the vagina, oviduct, and accessory vaginal pocket was not determined.

Buccal mass rather short, strongly curved on top, generative sac very small. Buccal retractors insert in U-shaped fan about  $\frac{1}{3}$  of way from posterior of buccal mass. Esophagus inserting nearly at mid-point of upper surface of buccal mass, very slender and thin-walled, extending through visceral hump past apex of pallial cavity. At this point, the esophagus expands into a funnel shape, entering stomach yet allowing room for positioning of intestinal loops. Esophagus entering stomach on lower inner whorl margin just above apex of pallial cavity. Stomach occupies nearly entire whorl, grossly expanded to cover outer and upper margins, extending apically to point below "Y" of hermaphroditic duct, intestine reflexing along base of whorl, about midway between inner and outer margin. Intestine running apically to apex of pallial cavity, looping across outer whorl margin and abutting on kidney, reflexing backward and downward along expanding margin of stomach, then looping upward on outer wall to parietal-palatal margin and passing forward as hindgut.

Digestive gland extending from tip of soft parts to apex of pallial cavity, greatly reduced in region occupied by stomach.

Salivary glands slender, white, lying along and surrounding esophagus. Salivary ducts entering buccal mass-esophagus junction laterally.

Free muscle system simple. Columellar retractor very large, buccal retractor uniting with tentaculars shortly before joining main tail fan.

(Based on FMNH 135421, Church Road, Kaitaia, Northland, New Zealand, L. Price! October 1962, several adults.)

### **Flammulina zebra (Le Guillou, 1842).**

*Description of soft parts.*—Foot and tail about equal in length to shell diameter, truncated anteriorly, rapidly tapering from about 1 mm. behind visceral stalk posterior. Sole undivided longitudinally, with weak transverse corrugations extending from sides of foot. Pedal grooves high on foot, suprapedal slightly weaker than pedal, united above tail, no caudal horn, or middorsal groove present. Slime network irregularly rectangular, relatively weak. Head and ommatophores without unusual features. Gonopore on right side of head, directly behind ommatophore.

Body color dark gray on head and tail, lighter between pedal grooves, soles and sides of foot yellow-white.

Mantle collar (fig. 29a, MC) without lobes or laps, no glandular extension onto pallial roof. Anus (A) opening slightly anterior to external ureteric pore (KX). Urinary chamber (LK) not differentiated.

Pallial region (fig. 29a) extending about  $\frac{1}{3}$  whorl apically, quite broad, lung roof without color markings. Kidney (K) bilobed, short, quite wide. Ureter (KD) thick, arms sharply angled, with angle approaching 80°. Heart (H) half length of kidney. Principal pulmonary vein (HV) weakly branched, stopping well short of mantle collar.

Hindgut (HG) slender, reaching parietal-palatal margin opposite point where ureter reflexes, then running forward to anus.

Ovotestis two large clumps of palmately clavate alveoli buried in digestive gland above stomach apex. Clumps with central orientation perpendicular to plane of coiling, laterally fanning from center. Hermaphroditic duct narrow, variously kinked and coiled, extending to side of prostate, reflexed upward and straightened to angled union with carrefour (fig. 29c–d). Albumen gland large, of slender acini, tightly packed around carrefour region. Talon (GT) very short, with circular head, buried in albumen gland. Carrefour (X) with only slight enlargement from talon shaft (fig. 29c–d). Prostate (DG) of comparatively few acini along sides of uterus, exact structure of passage from carrefour to vas deferens not determined. Possibly a narrow part of the uterine lumen serves to transfer sperm. Uterus (UT) grossly enlarged, twisted, with thick glandular walls. Vas deferens (VD) thicker for first  $\frac{1}{3}$  of length, then narrowed for last  $\frac{2}{3}$ , entering apex of epiphallus next to point where penial retractor muscle inserts, tightly bound to penis surface (fig. 29b). Epiphallus compacted into upper penial chamber (fig. 29e–i), with complex valvular entrance from vas deferens (fig. 29i–j). Penial retractor (PR) very short, scarcely a separate muscle zone. Penis (P) almost circular, about 1.3 mm. long, apex (fig. 29e) with compacted epiphallus opening through a corrugated verge (fig. 29e–f, PV), lower portion with a complex set of pilasters, highly modified from standard charopid pattern. Atrium (Y) long and slender, thin-walled, without internal sculpturing (fig. 29b).

Free oviduct (UV) short, twisted, fusing indistinctly with lower organs. Spermatheca (S) expanded basally, shaft following side of uterus, curving up and around carrefour region, head partly next to exposed section of prostate, partly next to albumen gland, oval in shape. Vaginal and lower penis area fused into a common chamber.

Free muscle system short, characterized by lack of fusion between muscles. Right ommatophoral retractor (TER) not passing through penioviducal angle, arising laterally from columellar muscle. Right rhinophoral retractor (TVR) arising from columellar muscle just inside origin of ommatophoral retractor.

Buccal mass shortly oval, proportionately very large, with small, generative sac. Buccal retractors split, each half inserting laterally near posterior margin of buccal mass, inserting at apex of columellar muscle. Esophagus short, not enlarged, arising from middle of buccal mass upper surface. Stomach starting expansion before apex of pallial cavity, occupying  $\frac{1}{2}$  whorl, then reflexing to intestine, which loops down and forward along lower whorl margin, looping inward and upward along side of pericardium and pericardial kidney, then making a curved U-loop backward and inward before angling forward as hindgut to parietal-palatal margin. Hindgut slanting down from parietal-palatal margin at point of ureter reflexion.

Digestive glands typical. Salivary glands lying on top and on either side of esophagus, partly fused medially.

(Based on FMNH 153217, Okuti Valley, Banks Peninsula, near Christchurch, New Zealand, F. Climo! March 7, 1965. Three dissected adults.)

### **Amphidoxa marmorella (Pfeiffer, 1845).**

*Helix marmorella* Pfeiffer, 1845, Proc. Zool. Soc. London, 1845, p. 125—Island of Juan Fernandez; Pfeiffer, 1847, Monog. helic. viv., 1, p. 66; Albers, 1850, Die Heliceen, 1st ed., p. 110; Pfeiffer, 1852, Syst. Conchol. Cab., 1, 19(2), pp. 129–130, pl. 88, figs. 17–19 (plate issued in 1850); Reeve, 1852, Conchol. Icon., *Helix*, pl. 113, fig. 649.

*Helix (Amphidoxa) marmorella* Pfeiffer, Tryon, 1887, Man. Conchol., (2), 3, p. 46, pl. 20, fig. 54.

*Amphidoxa (Amphidoxa) marmorella* (Pfeiffer), Pilsbry, 1893, Man. Conchol., (2), 9, pp. 39–40, pl. 7, figs. 10–12.

*Amphidoxa marmorella* (Pfeiffer), Odhner, 1922, Nat. Hist., Juan Fernandez and Easter Island, 3, pp. 229, 230–231, figs. 9–10 (radula and jaw).

*Description of shell.*—Shell small, with slightly more than 3 rapidly enlarging whorls (fig. 30a). Apex slightly emergent, penultimate and body whorl flatly coiled, H/D ratio 0.550. Apical whorls

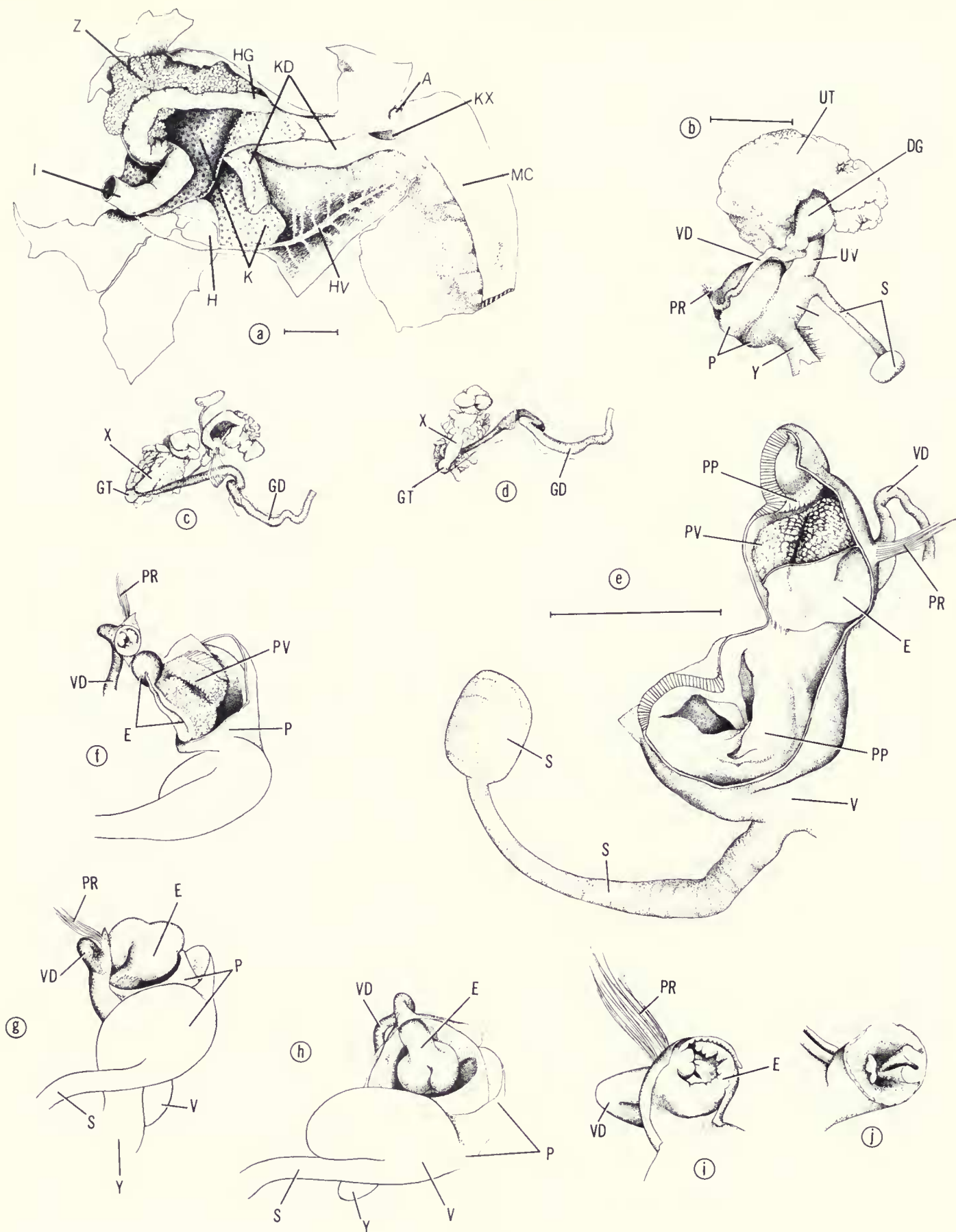


FIG. 29. Anatomy of *Flammulina zebra* (Le Guillou). Okuti Valley, Banks Peninsula, near Christchurch, New Zealand. F. Climo! III-7-1965. FMNH 153217: a, pallial region; b, postapical genitalia; c-d, views of the hermaphroditic duct-talon-carrefour junction; e, interior of penis chamber; f-h, detail of vas deferens-epiphallus-penis junction; i-j, detail of vas deferens-epiphallus junction. Scale lines equal 1 mm. for a-b, e; other figures greatly enlarged. (CW).



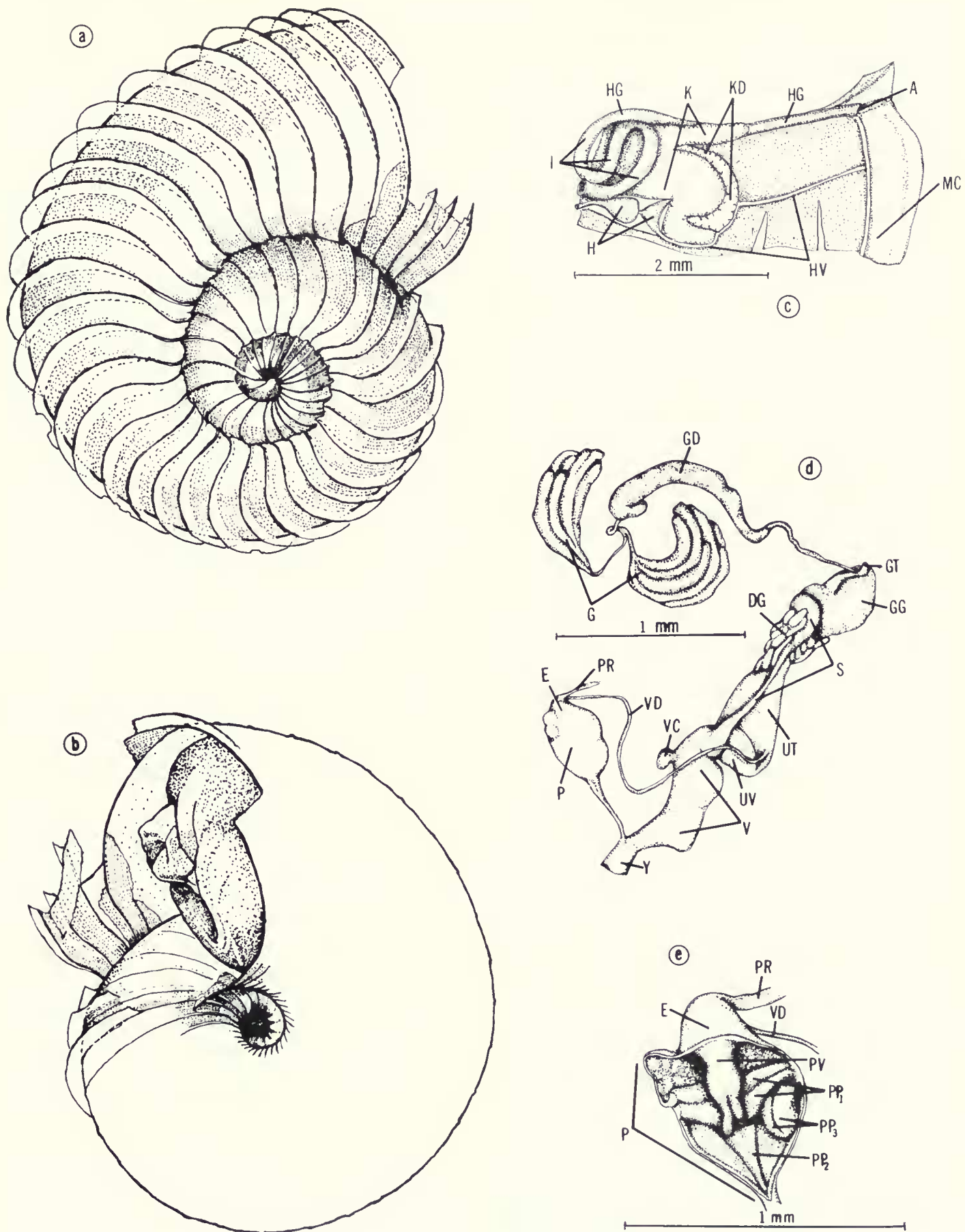


FIG. 30. Anatomy of *Amphidoxa marmorella* (Pfeiffer). 500 m. elevation, northeast slope, Portazuelo, Masatierra, Juan Fernandez. B. Malkin! IV-7-1962. FMNH 135424: a, apical view of shell prior to dissection; b, basal view of shell; c, pallial region; d, genitalia; e, interior of penis. Scale lines as marked. (PS).

1%, sculpture of 20 protractively angled large radial ribs over a microreticulated lattice visible only under 96 $\times$  magnification. Remaining whorls with protractively sinuated, lamellar radial ribs, 32 on the body whorl, whose interstices are more than 8 times their width. Ribs elevated greatly by periostracal extensions. Microsculpture a lattice of microradial and microspiral riblets, the former slightly stronger. Sutures deep, whorls rather flatly rounded above evenly rounded periphery and base. Color light yellow-white with very vague reddish flammulations, waved, becoming strongly retractive on base of shell, apparently not extending into umbilicus. Umbilicus narrow, V-shaped, regularly decoiling, contained 8.3 times in the diameter. Aperture large, subcircular, slightly flattened laterally above periphery, inclined about 30° from shell axis. No apertural barriers. Height of shell 1.64 mm., diameter 2.99 mm.

*Description of soft parts.*—Body completely retracted within shell (fig. 30b), soft parts relatively hardened and difficult to dissect. Foot relatively short and broad, rounded behind, apparently not tapering, truncated anteriorly. Sole undivided longitudinally, with rather strong transverse corrugations near tail, corrugations coming from slime network. Pedal grooves deep, high on foot, suprapedal as marked as pedal, both grooves uniting over tail. Because of contraction, presence or absence of middorsal groove could not be determined. Slime network a sharply defined irregularly rectangular network. Ommatophores short and chunky.

Body color yellow-white, mantle collar brownish. Eyespots small and black, upper part of stalk with black speckles.

Mantle collar (fig. 30c, MC) thick, glandular, without any mantle gland extension onto lung roof. Pneumostome masked by bulges in mantle collar, but no distinctive lobes present. Anus (A) opening at inner edge of mantle collar, a slight groove running from it to outer edge of collar.

Pallial region (fig. 30c) extending about  $\frac{1}{3}$  whorl, shape and positioning of structures probably altered by extreme contraction of animal. Lung roof clear, without dark speckling except in region of ureter and pericardium and a very few along hindgut near anus. Kidney (K) bilobed, main lobe pericardial, with a narrow tongue extending along hindgut (HG). Main lobe twisted in front of heart (H) extending on both sides of ureter (KD) tip. Base of kidney extending outside of intestinal loops along outer whorl edge (partly an artifact of contraction?). Entire first loop of intestine and part of loop to hindgut lying next to kidney. Ureter (KD) following anterior margin of pericardial kidney arm upward and slightly backward into small pocket between pericardial arm of kidney and hindgut then ending in a pore pointing apically. No groove leads toward pneumostome nor is there any trace of a secondary ureter. Heart (H) rather large, constricted by retraction. Principal pulmonary vein (HV) following edge of kidney and tip of ureter, then passing forward to mantle collar with no conspicuous lateral venation.

Ovotestis (fig. 30d, G) two clusters of finger-like lobes, some bifurcated, imbedded in digestive gland above stomach, a Y-fork collecting tubule attaching them to hermaphroditic duct (GD). Latter extending along stomach at basal margin of whorl, a thick, nodular, opaque, iridescent tube becoming slender near albumen gland and running to stalk of talon. Albumen gland (GG) finely textured, occupying visceral area between stomach base and apex of pallial cavity inside of intestinal loops. Head of spermatheca (S) lying in angle between prostate head and albumen gland base. Talon (GT) long with slender, slightly tapering head and broader base that is buried in albumen gland. Hermaphroditic duct entering talon below apex of slender stalk. Talon opening into apices of prostate and uterus. Prostate (DG) of large acini opening into a closed duct that is partly enfolded by uterus (UT). Lower part of prostate squeezed by expanded uterus and opening into slender vas deferens (VD). Uterus (UT) a slender, thin-walled tube above, opening into a grossly expanded chamber with thicker glandular walls and weak traces of ridging.

Vas deferens (VD) a very slender tube passing to penioviducal angle, around right ommatophoral retractor, then up to head of penis (P). Penial retractor (PR) arising on diaphragm, inserting on head of epiphallus (E). Vas deferens inserting laterally on epiphallus, which contains longitudinal pilasters surrounding the vas pore and leading into the verge (fig. 30e, PV). Penis proper bulbous above, tapering to

a slender duct before joining vagina (V) to form atrium (Y). Internally (fig. 30e) penis with a large apical verge (PV) whose tip is bifurcate; a large circular muscular collar (PP<sub>1</sub>) separated into two parts; a broad, thin pilaster (PP<sub>2</sub>) tapering to the slender basal stalk; and an apparently doughnut-shaped pilaster (PP<sub>3</sub>) that is partly folded over upon itself in the available specimen. Atrium (Y) short, rather large in diameter.

Free oviduct (fig. 30d, UV) short, only slightly narrowed from uterus, internally with glandular walls and vague pilasters. Spermatheca (S) with basal part of shaft slightly expanded, tapering along surface of uterus and prostate, expanded head lying in angle between prostate and albumen gland. Vagina (V) very large, expanded, internally with broad longitudinal glandular pilasters that continue into atrium (Y). No special pilasters or collars mark spermathecal or oviducal terminations. A small vaginal diverticulum (VC) is a blind pocket opening between two major pilasters that continue up into spermatheca.

Buccal mass ovoid, strongly contracted, generative sac rather large. Buccal retractor inserting in U-shaped fan about  $\frac{1}{3}$  of way from posterior end, not split. Esophagus entering top of buccal mass slightly behind midpoint, a rather thick tube with longitudinal pilasters following inner margin of whorl past apex of pallial cavity and entering stomach very shortly past that point. Stomach extending about  $\frac{1}{4}$  whorl, expanded to fill parietal and upper palatal walls almost immediately, narrowing about  $\frac{1}{3}$  of way from apex, the narrowing resulting in both a descension from the parietal-palatal angle and basal narrowing. At apex, stomach reflexes downward and turns near basal margin before joining intestine. At stomach-intestine junction, ducts of digestive gland enter on each side. Intestine following basal-palatal margin of whorl forward to base of kidney (fig. 30c, K), looping across kidney base, nearly touching hindgut, looping directly downward, then backward and upward as hindgut to parietal-palatal margin, finally following that margin to anus. Extreme sharpness of intestinal looping may be result of contraction.

Digestive gland extending from apex of soft parts to apex of pallial cavity; a broad band along lower palatal wall between intestine and outer part of stomach, reduced in amount in area of intestinal loops and albumen gland. Openings into stomach-intestine junction very prominent.

Salivary glands white, finely textured, lying lateral to esophagus, touching above. Ducts of salivary glands entering buccal mass on each side of esophageal insertion.

Free muscle system short and massive. Buccal retractor nearly as broad as long when contracted. Right ommatophoral retractor passing between penioviducal angle, uniting with rhinophoral retractor just before joining tail fan. Tentacular retractors joining tail fan subapically and laterally, buccal retractor joining medially and apically.

Jaw fragmented during mounting, composed of about 20 delicate plates that are weakly striated and do not strongly overlap.

Radula with 75 rows. Central tooth very small, with weak side cusps. Lateral teeth large, tricuspid, endoconal size gradually increasing during shift to marginals, ectocones on outer marginals split.

(Based on FMNH 135424, northeast slope at 500 m. elevation, above Portazuelo, Masatierra, Juan Fernandez, B. Malkin! April 7, 1962. One adult specimen.)

### **Stephanoda binneyana (Pfeiffer, 1847).**

*Description of soft parts.*—Foot narrow and rather elongated, not tapering posteriorly, bluntly rounded behind (fig. 31f). Pedal grooves deeply and equally impressed, high on sides of foot. Sole undivided longitudinally, but strongly corrugated perpendicular to body axis, such corrugations being continuations of lateral grooves below pedal grooves. Tail with middorsal groove, bell-shaped in cross section, sloping down to point where pedal grooves unite. No caudal foss or horn developed. Slime network fine, irregular, oblong to rectangular patches.

Body color in preservative pale yellow-white, sides of head and mantle with gray markings, ommatophores black.

Mantle collar (MC) thick with tapering edge (fig. 31a). Pneumo-



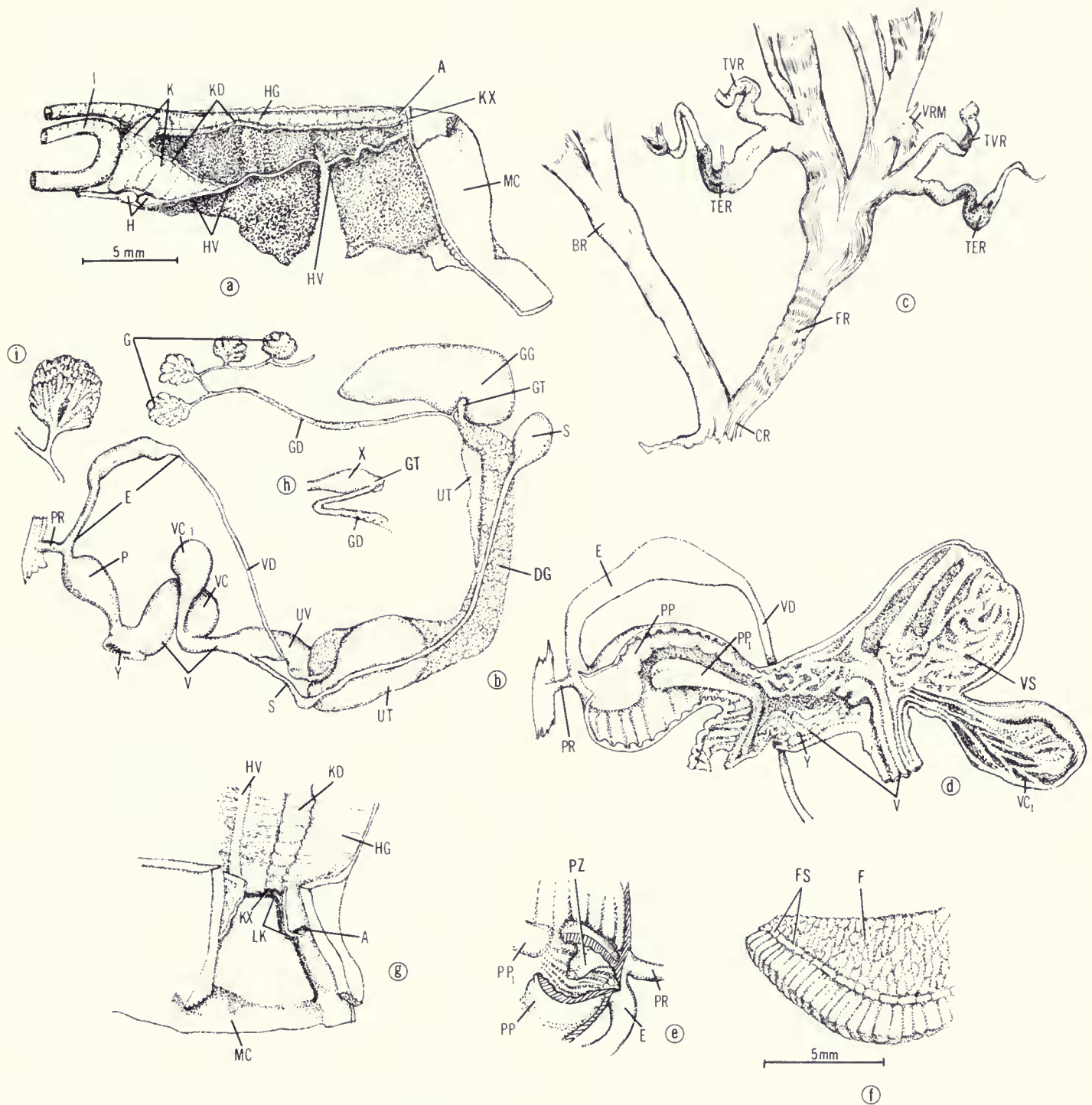


FIG. 31. Anatomy of *Stephanoda binneyana* (Pfeiffer). Rio Cisnes ( $44^{\circ} 45' S$ ,  $72^{\circ} W$ ), Prov. Aysen, Chile. L. E. Pena! II-1961. FMNH 135428: a, pallial region; b, genitalia; c, free muscle system; d, interior of terminal genitalia; e, detail of epiphallus-penis junction; f, rear portion of tail; g, detail of anterior mantle cavity; h, detail of hermaphroditic duct-talon-carrefour junction; i, lobe of ovotestis. Scale lines as marked, detail sketches greatly enlarged. (PS).

stome (LP) masked by small left anterior mantle lobe (MA). Edge of collar just anterior of pneumostome has a weak thickening forming an accessory mantle lobe (AMA). Anus, excretory pore, and pneumostome sharing common opening (fig. 31g). Anus (A) slightly anterior to external ureteric pore (KX). Urinary chamber (LK) a shallow groove running past anus and continuing (although less sharply defined) nearly to edge of mantle collar.

Pallial region (fig. 31a) elongated, but in view of contracted state no accurate estimate of length possible. Lung roof with variable coloring, speckled with widely scattered black and white flakes to nearly coal black. Kidney (K) short, elongately triangular with a

narrow, hooked basal extension abutting hindgut (HG). Base of kidney against loop of intestine. Ureter (KD) slender, sigmurethrous, flaring slightly midway along hindgut, arms of ureter widely separated by lung roof. Heart (H) slightly more than  $\frac{1}{2}$  length of kidney. Principal pulmonary vein (HV) angling toward pneumostome, nearly reaching mantle collar, without conspicuous side branches.

Ovotestis (G) imbedded in digestive gland above stomach-intestine reflexion, consisting of 8 sets (4 shown in fig. 31b) of clumped palmately clavate alveoli (fig. 31i) strung linearly along very thin hermaphroditic duct (GD). Ovotestis distinctly lighter in tone than digestive gland. Collecting tubule of hermaphroditic duct

very thin, bilobed. Main section a round muscular tubule, slightly iridescent in tone, narrowing just before base of albumen gland (GG), reflexing abruptly and ascending to apex of bilobed talon (GT) (see fig. 31h). Albumen gland elongately ovate, blunt-tipped, lying completely above pallial cavity, very fine-textured. Talon (GT) buried in albumen gland, quite small, white. Duct from talon opening into head of prostate-uterus without differentiated carrefour. Prostate (D) equal in width to upper portion of uterus, individual acini much larger than those of albumen gland. Lower part of prostate enveloped in basal sections of uterus. Uterus (UT) tripartite. Upper section narrow, sacculated, equal in width to prostate. Basal  $\frac{1}{2}$  of uterus surrounded by a hollow, smooth-walled, white-colored chamber with very fine texture. Basal section of uterus expanded into a chamber with lamellar walls.

Vas deferens (VD) originating from groove of prostate enfolded by second uterine chamber, a narrow tube passing down to penioviducal angle, then almost immediately into epiphallus (E). Latter a much larger muscular tube, first half swollen with strong pilasters on one wall, then narrowing to about 4 times diameter of vas deferens. Epiphallus entering penis (P) just below attachment of penial retractor (PR), which is short, quite thick, and originates on diaphragm. Penis rather short, apical half bulbous, tapering toward atrium. Internally (fig. 31d-e) with rather heavy and complex pilasters. A single large lamellar plate (PP) starts just below epiphallic pore, curves up and around it, then passes longitudinally down wall opposite insertion of penial retractor. A second longitudinal pilaster (PP<sub>2</sub>) arises below origin of major pilaster and tapers gradually toward atrium. A series of circular minor pilasters complete the armament.

Free oviduct (UV) short and muscular, bulbous, internally (fig. 31d) with rugose pilasters. Spermatheca (S) of long type, expanded head in visceral mass above pallial cavity and cephalic aorta, stalk very slender. Vagina (V) long, with twisted, bilobed accessory vaginal appendix (VC). Main lobe (fig. 31b, d) with muscular walls, a few longitudinal pilasters, and an intricately reticulated stimulatory pad (VS). Secondary lobe (VC) a bulbous, tapering, thin-walled organ, the expanded head with many lamellar plates. Stalk of secondary lobe and duct of vagina with weak longitudinal pilasters. Main accessory lobe of vaginal appendix bound to right side of tail fan muscle (fig. 31c, VRM) slightly less than halfway from union with right tentacular retractors and insertion on foot.

Free muscle system (fig. 31c) simple. Buccal retractor (BR) attaching on posterior  $\frac{1}{3}$  of buccal mass, in U-shaped fashion, but not split until very tip, and joining tail fan (FR) at site of columellar attachment (CR). Ommatophoral retractor (TER) and rhinophoral retractors (TVR) unite a short distance back and almost immediately fuse with tail fan. Right ommatophoral retractor passing between penioviducal angle. Tail fan split slightly posterior to junction with tentacular retractors (TR). Penis base bound to body wall, accessory lobe of vagina bound to right part of tail fan (VRM).

Buccal mass rather short and muscular, generative sac prominent. Esophagus entering top of buccal mass between  $\frac{1}{3}$  and  $\frac{1}{2}$  way from posterior end, large and muscular, with heavy longitudinal ridges anteriorly, tapering and becoming thin-walled to apical end of pallial cavity. Stomach a very large thin-walled sac extending less than 1 whorl apically, along parietal-palatal margin and occupying much of space in visceral hump. Reflexing as intestine along lower inner margin of whorl, running back to apex of pallial cavity, curving up and abutting on kidney base, looping back diagonally downward for  $\frac{1}{2}$  length of stomach, then reflexing forward diagonally as hindgut. Hindgut not reaching parietal-palatal margin until just above start of pallial cavity, following margin to anus and only slightly expanded in lower part of pallial cavity. Salivary glands paired, lying on each side of esophagus, touching above and below. Ducts very slender, inserting on each side of posterior esophageal base. Extreme duct coiling and nearness of glands to buccal mass probably result of extreme contraction.

Digestive gland extending from top of pallial cavity to apex of soft parts (which do not reach shell apex). Lower section with intestinal loops finger-like. Minor collecting tubules pass through spaces

between branches of ovotestis clumps. Major duct empties into base of stomach.

(Based on FMNH 135428. Rio Cisnes, Aysen, Chile, L. E. Pena! February 1961. Four dissected adults.)

All of these taxa agree in basic structures of the genitalia, pallial region, radula so far as observed, and muscle system. Their differences relate to visceral hump and compaction changes in the case of *Flammulina* and the *Otoconchinae*, multiple radiations between terrestrial and arboreal habitats (shell sculpture reduction, mucus pore intensification), and species recognition factors in the terminal genitalia. The latter changes are many and bewildering, since 15 to 30 endodontoids from a single locality is normal in New Zealand. The variations in penis interior structure illustrated by Climo (1969b, figs. 25A, 28D, 29B, C, 30E; 1970, figs. 16B, 20D, 21C) can be directly compared with the type of sympatric variations reported below.

Continuation of the *Otoconchinae* as a separate subfamily, based on the multiple changes in structure resulting from visceral hump reduction, can be justified and is accepted here. It is less strongly differentiated than the other subfamilies recognized in this report, and rigorous structural analysis may result in determining that the *Otoconchinae* is a grade in structure rather than a clade.

The remaining New Zealand Charopidae are not amenable to subfamily distribution at this stage. *Charopa*, *Phenacohelix*, and *Flammulina* agree in all essential details of structure. They are reasonably closely related. The many illustrations of Climo (1969a-b; 1970) do suggest possible subgroupings, but until details of vergic, epiphallic, and lower female tract structures are described and illustrated, no real decisions are possible. Although the New Zealand charopids have radiated extensively and confusingly, their basic structures seem rather coherent. Retention within an admittedly rather broad subfamily Charopinae is suggested pending detailed revisions.

Because most of the family names used for the Australian charopids have been based on New Zealand genera, the great variation found in these taxa will not be discussed further. Study of Western Australian taxa with primitive features is in progress (Solem, in preparation C). The family name Dipnelicidae Iredale (1937b, pp. 22-23) will be considered in that report. The structural variety in the Australian taxa seems greater than that reported for the New Zealand species, but this is only a preliminary impression.

The family Pseudocharopidae Iredale (1944, p. 312) was proposed by the phrases "An extraordinary development of beautiful small shells is indicated by this family name. . . . I was thinking of allotting them to the Flammulinidae, which they slightly resemble. . . . to save further confusion the above name (Pseudocharopidae) is utilized." Dissection of *Pseudocharopa lidgbirdi* (Etheridge, 1889) (fig. 32a-c) shows a typical pallial cavity configuration (fig. 32a), with bilobed kidney, complete secondary ureter, and essentially un-



branched pulmonary vein. The genitalia (fig. 32c) is unusual only in having a single kink in the hermaphroditic duct (GD), small prostate, shortened terminal female organs, the epiphallus shifted in relation to the penial retractor muscle, and the interior of the penis (fig. 32b) with high, smooth pilasters in the lower penis, rugose low pilasters in the upper penis. Because the shell of this species has a reduced visceral hump, most of the unusual features can be interpreted as secondary. The basic features are those of the Charopinae.

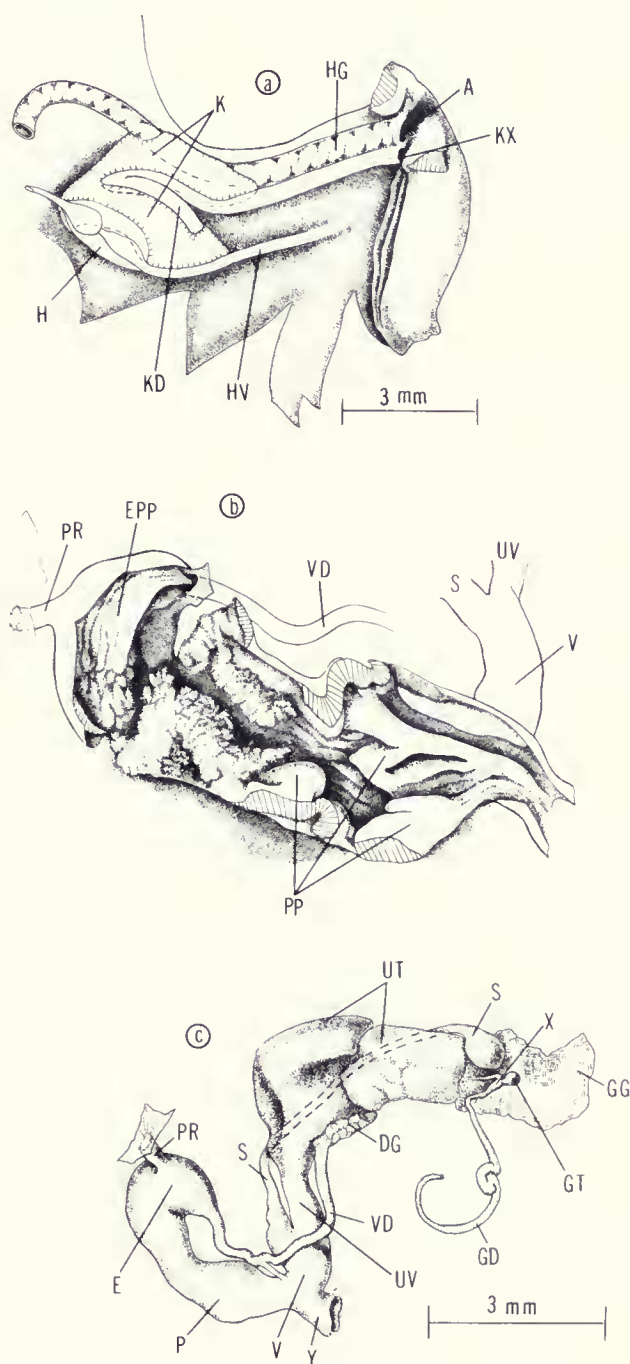


FIG. 32. Anatomy of *Pseudocharopa lidgbirdi* (Etheridge). Station 20, northeast slope of Mt. Lidgbird, 1,500 ft. elevation, south end Lord Howe Island. L. Price! IX-1963. FMNH 127977: a, pallial region; b, interior of penis complex; c, genitalia. Scale lines as marked; b greatly enlarged. (NB).

Amphidoxinae Thiele (1931, p. 578) is based on one of the Juan Fernandez Islands species, *Amphidoxa marmorella* (Pfeiffer, 1845). A single, retracted, nearly adult specimen (fig. 30a-b) was dissected. The genitalia (fig. 30d-e) has the typical charopid aspect, with the addition of a vaginal caecum (VC), shortened epiphallus (E), and internally shows the verge (PV), ring pilasters (PP<sub>1</sub>), and pocket stimulator (PC) seen in *Charopa* (fig. 9d) and *Sinployea* (figs. 43e, 57c). The only unusual features are the absence of a secondary ureter (fig. 30c) and the retention of a separate prostate. Despite this, the basic structures of *Amphidoxa* and *Charopa* are amazingly similar. At least the structures of *Amphidoxa* show how the Charopinae could be derived from more generalized stocks.

Traditionally, the South American genus *Stephanoda* has been associated with *Amphidoxa*. Dissection of *Stephanoda binneyana* (Pfeiffer, 1847) showed profound differences. The pallial region (fig. 31a) has the short rectal lobe found in *Phenacohelix* (fig. 11a), a complete secondary ureter (KD) that opens (KX) (fig. 31g) just posterior of the anus (A). In the genitalia (fig. 31b, d-e, h-i) the ovotestis consists of several follicle bundles (fig. 31b, i), the talon (GT) is reduced (fig. 31h), the prostate-uterus is typical, but the slender base of the spermatheca (S) (fig. 31b) and fat free oviduct (UV) again agree with *Phenacohelix* (fig. 11c). The tail of the animal (fig. 31f) has the typically conservative form found in *Charopa* (fig. 9a) and all Pacific Island taxa. The most unusual features are in the terminal genitalia, with a prominent vaginal caecum (VC) (fig. 31b), long vagina (V), and short penis (P). Internally (fig. 31d-e) the penis has circular pilasters and two large stimulators, but the epiphallus (E) enters through a pore rather than a verge (fig. 31e). There are irregular and complex pilasters within the terminal female genitalia (fig. 31d). In the absence of the verge and altered pilaster pattern, *Stephanoda* shows considerable similarity to structures seen in some of the non-verge bearing charopids illustrated by Climo (1969b, 1970). These structures emphasize that the charopids are a true Southern Hemisphere group and that relationships are somewhat complex.

Comments on a few other extralimital taxa are included under the appropriate subfamily discussions.

In this monograph I recognize five subfamilies in the Charopidae: Otoconchinae Cockerell, 1893; Rotadiscinae Baker, 1927; Charopinae Hutton, 1884; Trukcharopinae, new subfamily; and Semperdoninae, new subfamily. Of these, the Otoconchinae is least sharply differentiated, and the Charopinae is deliberately the most broadly defined, pending adequate anatomical revisions of the New Caledonian, New Zealand, Australian, South American, and South African taxa. Undoubtedly the Charopinae will be subdivided further in the future, but whether on a tribal basis or into several subfamilies will depend upon the results of future investigations. A brief diagnosis of each subfamily follows.

Subfamily Otoconchinae—Tail and body greatly elongated, visceral hump reduced with shell a cap or fragment, head shortened in relation to body length. Jaw fused, arcuate. Radula typical of Charopinae. Pallial region modified Charopinae because of shortening, genital system compacted by head and visceral hump reduction, basically Charopinae in structures. *Otoconcha* Hutton, 1884, and *Maoriconcha* Dell, 1952, are the included taxa.

Subfamily Rotadiscinae—Small to minute species with apical sculpture of short spirally arranged segments (fig. 4a–e), visible optically as spiral cords, postapical sculpture typically charopid. Jaw of separate plates. Radula usually typical except for ectoconal marginal splitting. Pallial region without to with a complete secondary ureter, kidney weakly to evenly bilobed. Ootestis of one to two clumps of short to long follicles, talon short to long, not with circular head. Terminal female system simple, sometimes with accessory caecum, relatively thin. Epiphallus usually below penial retractor insertion, short, opening into penis through a short conical verge or simple pore, walls of penis with longitudinal pilasters. *Rotadiscus* Pilsbry, 1926, *Radiodiscus* Pilsbry & Ferriss, 1906, *Radioconus* H. B. Baker, 1927, *Radiodomus* H. B. Baker, 1930, *Microcharopa*, new genus, and probably some undescribed genera from Western Australia are the included taxa.

Subfamily Charopinae—Small to large species with apical shell sculpture of spiral cords, radial ribs, or secondarily smooth, postapical sculpture typically charopid, frequently secondarily reduced. Apertural barriers developed in several lineages. Jaw of separate plates in smaller taxa, fused partly to completely in large. Radula generally with tricuspid laterals and marginals, but modified to bicuspid or unicuspid laterals and sometimes with ectoconal splitting on the marginals. Genitalia highly variable, epiphallus normally present, terminal genitalia normally thick at least in part, penis with or without verge, normally with complex stimulatory pilasters. As a temporary measure, all charopid genera not specifically assigned to other subfamilies are lumped in the Charopinae.

Subfamily Trukcharopinae—Small to medium-sized species with apical sculpture of spiral cords, postapical sculpture strong to secondarily reduced. Aperture with or without barriers. Jaw and radula typically charopid. Genitalia unusual in lacking an epiphallus. Vas deferens passing through the penial retractor muscle before entering the penis either through a verge or pore. Interior of penis with stimulatory pilasters of varied form. *Trukcharopa*, *Kubaryellus*, *Russatus*, *Roimontis*, *Palikirus*, *Jokajdon*, and *Palline*, new genera from Micronesia, are the included taxa.

Subfamily Semperdoninae—Medium-sized to large species with spiral apical cords, typical to greatly reduced postapical sculpture. Aperture with or without barriers. Jaw and radula without unusual features. Pallial region typical, with some variation in kidney lobe lengths. Genitalia unusual in the altered penis complex. Penial retractor inserting on head of epiphallus, which is a coiled double tube, outer wall thin muscle sheath, inner a thick glandular tube rolled inward on one side, opening into penis through a simple pore. Penis with an outer heavy muscle sheath of circular fibers that extends up around the lower epiphallus, with an inner tube containing fine longitudinal pilasters above that usually coalesce into 3 glandular pilasters below. *Semperdon*, *Ladronellum*, and *Himeroconcha*, new genera from Micronesia, are the included taxa.

The affinities of the subfamilies are still uncertain. The New Zealand Otoconchinae is an obvious sluglike secondary derivative from the New Zealand Charopinae. In structure it shows only minor differences. The Trukcharopinae from Micronesia are derivable from the typical *Charopa-Sinployea* stock by loss of the epiphallus and specialization of the penial surfaces. At present there are no Australian or New Zealand structural equivalents known, but I would not be surprised if relatives turn up in this area. The Semperdoninae from Micronesia have a very different penis structure than anything I have seen elsewhere.

Other features of their anatomy are compatible with derivation from the Charopinae, and finding relatives in a remote area of the family range would not surprise me in the least.

In contrast, the Rotadiscinae have a relict (Idaho, Arizona-Costa Rica, Trinidad, probably South America), Fiji, Western Australia (Solem, unpublished data) distribution. Their anatomy has a punctid aspect in part to the ootestis, the pallial region is more primitive than that of the Charopinae, and its slender terminal genitalia with some accessory organs is very different from the Punctidae and most of the Charopinae. This group may prove to be a relatively base stock of the charopid radiation.

Further phylogenetic comments are postponed pending completion of work on the Western Australian radiation and additional work on New Caledonian and Tasmanian taxa. Comments on relationships within subfamilies are given below.

### Subfamily ROTADISCINAE

A more expanded definition and discussion is postponed until completion of the Australian work. Inclusion of *Microcharopa* in the Rotadiscinae is based on its unique apical sculpture (fig. 4c–e) that is shared with *Radiodiscus* (Solem, 1977b, pp. 150–154, figs. 7–8), *Rotadiscus*, and undescribed Western Australian material. *Microcharopa* could not be dissected. In shell features it differs in its very small size and reduced whorl count, finer and more crowded radial ribs, and wide umbilicus. All of the New World genera are considerably larger, more coarsely ribbed and generally more variously umbilicated.

### Genus *Microcharopa*, new genus

Shell minute, with less than 3½ tightly coiled whorls. Apex and spire slightly elevated, body whorl descension a little more rapid. Apical sculpture (fig. 4a–e) of short, twisted, open-ended ridges arranged in 16–20 spiral rows on top of a weakly and broadly undulating radially ridged surface. Postnuclear whorls with narrow, very crowded, protractively sinuated radial ribs. Microsculpture of very fine radials, finer spirals, and some weak secondary spiral cords. Umbilicus widely open, cup-shaped, regularly decoiling, margins weakly shouldered. Whorls almost evenly rounded, slightly compressed laterally above periphery and on basal margin. Aperture without barriers or heavy callus. Anatomy unknown.

*Type species.*—*Microcharopa mimula*, new species.

Despite attempts on two different occasions to collect material on Lami Ridge and near Sigatoka, Viti Levu, no specimens could be found. Because only dead material was collected previously, the anatomy of this very unusual species could not be studied. Even under 100× magnification with the light microscope, the apex looks like it has only slightly wavy spiral cords, more frequent in number than with most species, but not very unusual in appearance. Scanning electron microscope photographs at 300×–10,000× magnification (fig. 4a–e) show that the apical sculpture is very complex. Instead of continuous spirals, there are relatively short segments that are equal in width to the



vague radial undulations (fig. 4a). Each individual segment starts as a cord, twists up and over, then ends as a cuplike structure (fig. 4d–e). These are in spiral rows and are present except for the first quarter apical whorl (fig. 4c), which seems to have low spiral cords instead. Postnuclear sculpture (fig. 4b) shows no really significant difference from that found in many Charopidae.

Separating *Microcharopa* from other Pacific genera is simple. The smallest *Sinployea* that has been dissected, *S. inermis lakembana*, is more than twice the diameter of *Microcharopa*, 2.36 mm. compared with 1.07 mm., and the smallest species assigned to *Sinployea*, *S. ellicensis nukulaelaeana*, is 2.08 mm. in mean diameter, only slightly less than twice the size. Species of *Vatusila* are in the 1.65–1.88 mm. size range, but these have very prominent apertural barriers and much simpler apical sculpture. The only genus in which the shells are approximately equal in size is *Discocharopa* (p. 59). Populations of that taxon average about 1.37 mm. in mean diameter and have  $3\frac{1}{2}$ –4 whorls, an even wider umbilicus, and, most important, very different apical sculpture (fig. 5a–c, p. 16).

The peculiar apical sculpture is shared with *Radiodiscus* (see Solem, 1977b, p. 152, figs. 7–8), which differs in having  $3\frac{3}{4}$ –4 $\frac{1}{4}$  whorls, reaches 2.0–2.25 mm. in diameter, and has about 21 ribs/mm. on the body whorl, compared with 36.5 ribs/mm. in *Microcharopa*. The narrower umbilici and larger sizes of *Rotadiscus* and *Radiodomus* are easy recognition features of these genera.

Only the one species, *Microcharopa mimula*, which is widely distributed in the Lau Archipelago and on Viti Levu, is known. The name *Microcharopa* refers to the very small size of this species and its resemblance in shape to the historical usage of the name *Charopa*.

***Microcharopa mimula*, new species. Figures 4a–e; 33a–c.**

**Diagnosis.**—Shell minute, diameter 0.95–1.13 mm. (mean 1.07 mm.), with  $3\frac{3}{4}$ – $3\frac{3}{4}$  rather tightly coiled whorls. Apex and spire slightly to moderately and evenly elevated, body whorl descending slightly more rapidly, spire protrusion about  $\frac{1}{6}$ – $\frac{1}{5}$  body whorl width, H/D ratio 0.400–0.469 (mean 0.449). Apical sculpture of 16–20 (mean 17.8) prominent, crowded spiral cordlike structures. Postnuclear sculpture of narrow, crowded, fine, sharply defined, protractively sinuated radial ribs, 117–136 (mean 126.6) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 32.3–40.5 (mean 36.5). Microsculpture of barely visible radial riblets, 1–2 between each pair of major ribs, equally fine spiral riblets, with occasional traces of weak secondary spiral cording. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.43–3.05 times (mean 2.68) in the diameter, margins weakly shouldered. Whorl contours almost evenly rounded, slightly compressed laterally above periphery and on basal margin, aperture circular, inclined about 10° from shell axis.

The similarities in size and shape to *Discocharopa* are marked, but the spiral apical cording and absence of a deeply recessed parietal lamella immediately separate *Microcharopa mimula* from that genus. Other barrier-free Fijian Charopinae are at least twice the

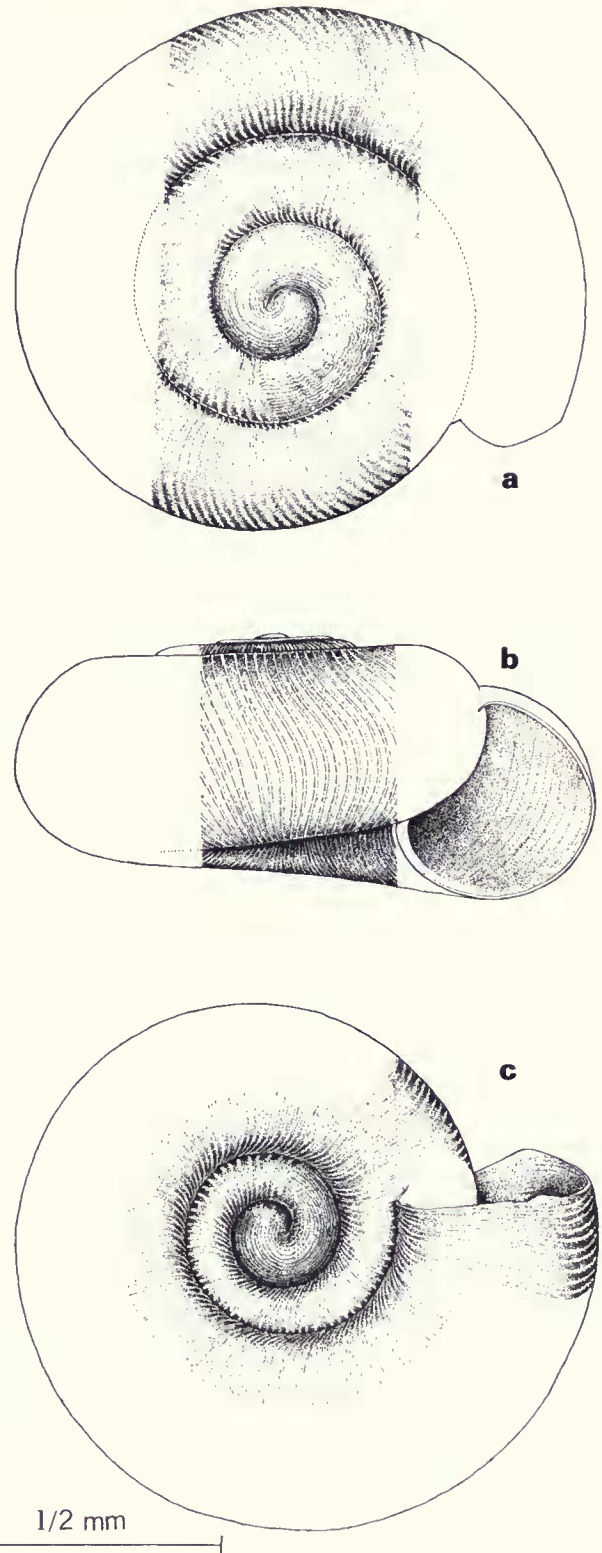


FIG. 33. a–c, *Microcharopa mimula*, new species. Lami Ridge, west of Suva, Viti Levu, Fiji. Holotype. BPBM 178490. Scale line equals 0.5 mm. (MM).

size of *M. mimula* at  $3\frac{1}{2}$  whorls and show numerous alterations in sculpture and shape.

**Description.**—Shell minute, with  $3\frac{3}{4}$  rather tightly coiled whorls that very slightly increase in width. Apex and spire slightly and evenly elevated, body whorl descending moderately, H/D ratio 0.467. Embryonic whorls slightly less than  $1\frac{1}{2}$ , sculpture of 18 crowded

spiral riblets, sinuated where crossing low, broadly rounded, relatively vague radial swellings. Postnuclear whorls with protractively sinuated, crowded, narrow, lamellar radial ribs, 136 on the body whorl, whose interstices are 1–2 times their width. Microsculpture as in diagnosis. Sutures deep, whorls shouldered above, gently and evenly rounded on outer margins. Umbilicus broadly open, saucer-shaped, regularly decoiling, contained 2.70 times in the diameter, margin weakly shouldered. Color very light yellow-brown. Aperture circular, strongly rounded near periphery and at baso-umbilical margin, inclined about 10° from the shell axis. Height of holotype 0.48 mm., diameter 1.02 mm.

*Holotype*.—Fiji: Viti Levu, Station 47, Lami ridge, 5 miles west of Suva, at 5–150 ft. elevation. Collected by Yoshio Kondo and C. M. Cooke, Jr., on July 24, 1938. BPBM 178490.

*Range*.—Munia, Mothe, Wangava, Nayau, Namuka, and Yangasa Levu, Lau Group, and Viti Levu, Fiji.

*Paratypes*.—Viti Levu: Near Sigatoka, ½ mile inland, under dead leaves, 50 ft. elevation (6 specimens, BPBM 88524, BPBM 88562); Sigatoka, near base of limestone cliff, ½–1½ miles from shore (1 specimen, BPBM 87930); Nayavu, upper Wainibuka River, 14 miles inland, 190 ft. elevation (1 specimen, BPBM 87959); Lami Ridge, 5 miles west of Suva (Station 47), limestone ridge, 5–150 ft. elevation (3 specimens, BPBM 178490).

Lau Group: Munia, ½ mile inland (Station 65), hillside in copra plantation at 600–900 ft. elevation (2 specimens, BPBM 179323); Mothe, central wooded peak, on leaf mold at 590 ft. elevation (4 specimens, BPBM 78585); Wangava, probably Station 27 (4 specimens, ex BPBM 166994); Nayau, Nauko (Station 43), hillside ½ mile inland at 250 ft. elevation (4 specimens, BPBM 167231); Namuka, Matandolo (Station 2), north-central point of island on hillside 500 ft. inland at 65–75 ft. elevation (2 specimens, ex BPBM 166614); Yangasa Levu, south end of island (Station 30), hillside, 150 ft. inland at 40 ft. elevation (2 specimens, ex BPBM 167137).

*Remarks*.—The extremely small size, widely open umbilicus, and very crowded sculpture easily separate *Microcharopa mimula* from all other Fijian endodontoids. It is most similar to the Melanesian-Polynesian *Discocharopa* in size and form but obviously differs in its spiral apical sculpture and the lack of parietal barriers. The wide distribution recorded above is undoubtedly very incomplete because the minute size of this species would result in its discovery by only the most diligent collector.

#### Subfamily CHAROPINAE

A brief diagnosis of the Charopinae was given on p. 70. It undoubtedly will be extensively modified when taxa extralimital to this study are reviewed. Because so few genera have had details of their terminal genitalia described or figured, I have not attempted to split the Charopinae into smaller clusters of genera. I can emphasize that eventual generic clusters will in-

clude taxa from highly diverse geographic areas and will deny many traditional associations. For example, the basic anatomical structures of *Notodiscus* Thiele, 1931, found on Kerguelen and other Subantarctic islands (Solem, 1968c), are very close to those seen in *Phenacohelix* Suter, 1892, from New Zealand (fig. 11); the structures seen in *Graeffedon* from Samoa (fig. 87) are matched closely by those found in *Helenoconcha relicta* Solem, 1977, from St. Helena (Solem, 1977c) and differ markedly from any Austro-Zelandic taxa dissected to date; *Amphidoxa* Albers, 1850, from Juan Fernandez (fig. 30a–e) shows a combination of basic Charopinae and unusual features and is quite unlike the anatomical pattern of *Stephanoda* Albers, 1860 (fig. 31a–i), from Chile, which was treated as a subgenus of *Amphidoxa* by Pilsbry (1893–1895, pp. 39–41), Thiele (1931, p. 575), and Zilch (1959–1960, pp. 221–222). The last commentator on these two genera, Odhner (1922, pp. 230–233, figs. 8–13, pl. 9, figs. 33–35), described the jaw and radulae of several Juan Fernandez species, plus an external view of the genitalia in "*Stephanoda quadrata*." Structures of the latter agree quite closely with the data presented here on *Amphidoxa marmorella* (Pfeiffer, 1845). Probably the Juan Fernandez "*Amphidoxa* and *Stephanoda*" of Odhner (1922) are monophyletic and best lumped under *Amphidoxa*. They are quite distinct from the Chilean *Stephanoda*. Given the above diversity and uncertainty, no firm allocations into clusters are possible.

Fortunately, the Pacific Island taxa, with three exceptions, appear to be a monophyletic unit. *Discocharopa* Iredale, 1913, with a Philippine to Society Island range, *Lagivala*, known from Indonesia to Fiji and the Ellice Islands, and the endemic *Graeffedon* from Samoa and Tonga show major differences from the other Charopinae. The remaining genera, insofar as they have been dissected, belong to the same basic stock as the New Zealand *Charopa* Albers, 1860, and presumably will remain Charopinae regardless of future revisions.

*Discocharopa* differs in shell microsculpture (figs. 5a–f, 37d). The only partial knowledge of its genital anatomy (fig. 34a–d) makes relating it to other taxa difficult. The extent to which the minute shell size (mean diameter 1.36 mm.) has resulted in slenderization and/or simplification of the anatomy is unknown. As discussed below (p. 75), a degree of similarity to the structures of *Phenacohelix pilula* (Reeve) (fig. 11a–e) exists, but their degree of relationship is unknown.

*Lagivala* has not been dissected and has an extensive extralimital range, with species known from Indonesia, New Guinea, and the Bismarck Archipelago. The extent of its relationship to the Philippine-Indonesian problematic genus *Beilania* Preston, 1913, is uncertain (see p. 184). Whether *Lagivala* is convergent with the New Zealand *Mylesia* (Climo, 1978) and *Ptychodon* Ancey, 1888, will require detailed comparisons that are beyond the scope of this report. It is only



possible to state that in barrier structure, distribution, and basic shell features, *Lagivala* is not similar to other Pacific Island genera.

*Graeffedon* differs quite dramatically in its anatomy (p. 200) and has very different barrier structure (p. 17). It is clearly related to the St. Helena endemic, *Helenoconcha*, and probably will receive eventual subfamily separation.

Of the remaining Pacific Island Charopinae, adequate anatomical data is available for *Sinployea*, *Ba*, and *Tuimalila*, fragmentary data for one species of *Vatusila*, and no data on the anatomy of the monotypic *Maafu* and *Lauopa*. The anatomical features of the Pacific Island genera agree with those of *Charopa* (figs. 9a–g, 10) in the basic pallial structure (except for the lack of a glandular extension onto the pallial roof) and the components of the interior terminal genitalia. The penes have a verge, pocket stimulator, and circular ridges. The lower female tracts have complex valvular arrangements at the free oviduct and longitudinal pilasters (compare figs. 9d and 57f). As pointed out above (pp. 27–29), the relative prominence of these penial complex structures differs dramatically from species to species under conditions of sympatry, but the presence of the same exact structural elements in *Charopa*, *Sinployea*, *Tuimalila*, *Ba*, and such extralimital taxa as *Amphidoxa* (fig. 30e), *Pilsbrycharopa* (see Solem 1970a, fig. 2i), and *Pseudocharopa* (fig. 32b) indicate that this is a basic pattern. The lengthened terminal female organs of *Charopa* (fig. 9b) are a minor change of little or no phyletic significance. *Charopa* (fig. 10) differs from Pacific Island taxa most noticeably in the comparatively simple entrance of the vas deferens into the epiphallus. This contrasts with the elaborate valve seen in *Sinployea* (fig. 57e). Despite the extreme compaction of its genital system, the New Zealand *Flammulina* shows the same basic internal elements of the penis (fig. 29e) and has a complex vas deferens-epiphallus junction (fig. 29i–j) equivalent to that seen in the Pacific Island genera.

Without added reference dissections of extralimital taxa, attempts to propose a phylogenetic tree for the Charopinae are premature. The important point here is that many Pacific Island genera are clusterable with New Zealand, New Guinea, Lord Howe Island, and Juan Fernandez genera. That their degree of relationship and phylogenetic order cannot yet be ascertained is a secondary problem.

Just in reference to the Pacific Island taxa grouped here, *Sinployea* is most generalized, with *Ba* an obvious specialization from an ancestor very similar to if not actually the extant species *Sinployea irregularis* (Garrett). The Tongan *Tuimalila* is an experiment in increased whorl width and gigantism also derivable from a *Sinployea* ancestor. Both *Maafu* and *Lauopa*, neither of which have been dissected, present problems. *Maafu* shows great conchological specializations, but can be derived from the *Sinployea inermis* groups found in the same area. Its changes are of the same

order of magnitude found in the Lau Archipelago Endodontidae radiation of *Zyzyxdonta*, *Priceconcha*, and *Thaumatodon* (Solem, 1976b, pp. 461–467), and this is interpreted as a local experiment. *Lauopa*, known from limited subfossil material, is grouped here for convenience but conceivably could be an outlier of the Semperdoninae (see p. 177). The data needed to determine its affinities are not available. *Vatusila* has only a fragment of its anatomy known, but the penis structures (fig. 84a–b) are matched almost exactly by those seen in *Sinployea aunuuana* (fig. 53c). I am confident that *Vatusila* is correctly associated. Similarities in barrier size, shape, and positioning (figs. 82–83, 85) to some of the New Zealand *Ptychodon* and *Fectola* (Climo, 1978, figs. 3–4, 7–8) are intriguing, but deciding whether this is convergence, parallelism, or genealogy is beyond the scope of this review. Within *Vatusila*, there is a trend toward barrier reduction (see p. 192) and wider spacing of the radial sculpture. Although it would be tempting to suggest because of this that *Vatusila* might represent the ancestor of *Sinployea*, I suspect that they do not have a direct ancestor-descendant relationship but represent two independent colonizations of the Pacific Islands.

Thus, of the Charopinae on the Pacific Islands, I interpret *Ba*, *Tuimalila*, and *Maafu* as local direct derivations from *Sinployea*, with *Vatusila* an independent colonization. *Lauopa* is of uncertain status, whereas *Discocharopa*, *Lagivala*, and *Graeffedon* also represent independent colonizations of the Pacific Islands. Because there are several independent colonizations where external affinities are unknown, preparation of phylogenetic trees equivalent to those of the Endodontidae (Solem, 1976b, pp. 110–111, figs. 57–58) was not attempted.

The fossil evidence is meager but intriguing. *Vatusila eniwetokensis* (Ladd, 1958) is a Miocene species from Eniwetok in the Marshall Islands, whereas extant species are found in Lau Archipelago, Tonga, Niue, and Vaitupu, Ellice Islands. *Lagivala davidi* (Ladd, 1968) is a Late Pleistocene or Recent fossil from Funafuti, Ellice Islands. Extant species are known from Indonesia, New Guinea, New Britain, and Viti Levu. The genus has not been recorded from the Solomon Islands, New Hebrides, or New Caledonia. The Funafuti species is very closely related to the Fijian *L. vivus*. The Marshall Islands' Miocene *Vatusila* is matched by the Miocene *Cookeconcha subpacificus* (Ladd, 1958) and the Pliocene to Pleistocene *Minidonta inexpectans* (Ladd, 1958) from Bikini, Marshall Islands. All three genera show a shrunken post-Miocene range correlating with the changing of the Marshall Islands from high islands to atolls (see Solem, 1976b, pp. 117–118). The distributional shift is thus interpreted as range contraction, rather than the more simplistic assumption of migration.

Better understanding of the Pacific Island Charopinae relationships requires more intensive investigation of the Lau Archipelago, especially to obtain

anatomical material of *Lauopa* and *Maafu*, combined with analysis of extralimital genera.

The generic ordering used below places two of the "convenience-grouped" genera first (*Discocharopa*) and last (*Graeffedon*), with *Lagivala* sited for comparative purposes next to *Vatusila*. Detailed discussions of variation within and among genera are grouped under the appropriate generic discussions rather than here.

### Genus *Discocharopa* Iredale, 1913

Proc. Malacol. Soc. London, 10 (6), pp. 379–380.

Shell minute, with slightly more than  $3\frac{1}{2}$  normally coiled whorls. Apex and spire usually slightly to moderately elevated, body whorl descending more rapidly. Apical sculpture of major radial ribs more crowded near end of apex, with periostracal, relatively regular folds providing a microspirial element. Postnuclear whorls with narrow, sharply defined, crowded, strongly protractively sinuated radial ribs. Microsculpture of very fine radial riblets with serrated edges, no trace of spiral sculpture. Umbilicus very widely open, saucer-shaped, regularly decoiling, margins rounded. Whorls flattened laterally above and below rounded periphery. Color white with a yellow tinge. Aperture with or without a small to very large and deeply recessed, medial parietal barrier. Pallial region with complete secondary ureter, kidney bilobed, pericardial lobe longer than rectal. Genitalia with short bilobed ovotestis, slender talon. Terminal genitalia slender with subapical entrance of vas deferens, no externally recognizable epiphallus, penis internally with longitudinal pilasters.

*Type species.*—*Charopa* (*Discocharopa*) *exquisita* Iredale, 1913, by original designation.

The shell sculpture of *Discocharopa* (figs. 5a–f, 37d) is quite different from that found in any other Pacific Island Charopidae. Like the Endodontidae, the apical whorls (fig. 5b–c) have prominent radial ribs that become quite crowded near the nuclear-post-nuclear boundary (fig. 5a), but the microsculpture is quite different from that seen in the Endodontidae. The latter have very fine, regular, "squiggly" microspirals that continue onto at least the early postnuclear whorls (Solem, 1976b, p. 38, fig. 28c–e; p. 39, fig. 29a). The Charopidae have fine to prominent spiral cords (for example *Sinployea modicella*, fig. 1a–c, p. 10) with weak to strong (fig. 2c, p. 11) secondary radial elements. *Discocharopa* has spiral sculpture that is of irregular shape, length, spacing, and angle of orientation. Similar apical sculpture has been found in several New Zealand species usually classified in *Ptychodon* (for example, *P. microundulata* in Solem, 1970b, pl. 58, figs. 4–6) but now referred to *Mylesia* (see Climo, 1978, p. 185). The postnuclear sculpture in *Discocharopa* differs from all endodontoids examined to date. All these have both microspirial and microradial elements, but *Discocharopa* (fig. 5b, d–f) shows no trace of microspirial elements, and the radial sculpture has unusual features. The major ribs (fig. 5a–b, d–f) retain remnants of microradial clustering on their apices only on early postnuclear whorls (a–b), whereas the latter whorls (d–e) appear to have a "rolled" or expanded rib peak. The microradials (e–f) are partly broken up into irregular short segments by transverse grooves. The

latter have no counterpart in any Pacific Island species examined to date.

After considerable effort over many years, it was possible to obtain material and partially work out the basic anatomy of *Discocharopa*. The wide range of *Discocharopa* yielded hope of borrowing material to dissect, and fieldwork by L. Price in Fiji and by Price and Solem in Australia could have produced live material. No material was obtained until two specimens from the National Museum, New Zealand, were provided for study by their collector, Frank Climo. They were collected "behind the landing," Raoul Island, Kermadec Islands, on August 24, 1972, and thus represent near topotypic material of the genotype, *Discocharopa exquisita* (Iredale, 1913, pp. 379–380), which was described from "Sunday Island, Kermadec Group. Living under rotten wood, stones, etc."

Both examples had completely retracted within their shells, and the albumen gland had crystallized, which made interpretation of most structures difficult. The main uncertainties include whether the prostate-uterus are combined or separated, the talon structure, and the position and shape of the spermathecal head. I suspect that the latter is bound into the aorta at the area where the kidney base and albumen gland touch the diaphragm. In neither specimen was I successful in separating the kidney base, albumen gland, intestines, and hindgut because of extensive albumen gland crystallization. Undoubtedly the spermathecal head was mangled and lost in the attempts to work out structures in this area. The exact shape, size, and relationship of the talon to the hermaphroditic duct could not be determined precisely. Figure 34b represents the best interpretation of dissector and illustrator, but could be incorrect.

The ovotestis (fig. 34a, G) is unusual in that it lay alongside the stomach and below the main area of digestive gland. The bilobed condition is found in many charopids, but the anterior shift in position has not been seen by me in other taxa. The hermaphroditic duct (GD) was iridescent, again as in many charopids, and the albumen gland was deeply dented by loops of the intestine, thus having a very irregular shape. A swollen uterine area was clear, but the prostate tissue was very small and the spermathecal shaft closely bound to the margin. Because of partial crystallization in the uterine area, details could not be worked out. The vas deferens broke and is shown (VD) reflexed, but the long vagina and penis have been unfolded in order to show a little more detail (fig. 34c). The entrance of the vas deferens into the penis is subterminal, with a short penial retractor muscle inserted apically. Apparently there are at least two longitudinal pilasters within the penis, but exact structures are too small to be determined from available material.

The pallial region (fig. 34d) has a closed and complete secondary ureter (KD); the kidney (K) is bilobed with a large section touching to partly overlapping the



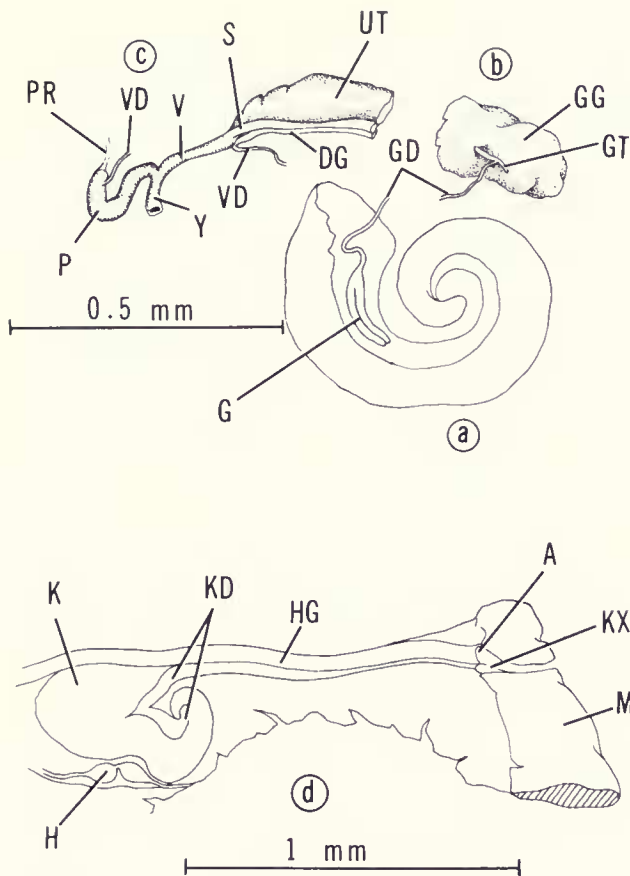


FIG. 34. Anatomy of *Discocharopa aperta* (Möllerndorff). Forest behind landing, Raoul Id., Kermadec Islands. F. Climo! VIII-24-1972. FMNH 193764: a, ovotestis; b, detail of talon and carrefour; c, post-apical genitalia; d, pallial region. Scale lines as marked. (EL).

hindgut (HG). Details of the anus (A) and external ureteric pore (KX) are only approximate. The apex of the kidney is curved over around the start of the ureter, possibly as a result of retraction into the shell.

The larger of the two dissected specimens was 0.62 mm. high, 1.51 mm. in diameter, H/D ratio 0.413, whorls 3%, umbilicus 0.43 mm. wide, D/U ratio 3.54. The more successful dissection was made on the smaller example, which was 0.58 mm. high, 1.25 mm. in diameter, with 3% whorls.

All observed anatomical features are consistent with *Discocharopa* being a member of the Charopinae. Unfortunately the small size, contraction, and partial crystallization combined to prevent full study. Whether the slender terminal genitalia is a secondary specialization is uncertain. Unquestionably the features observed are different from *Sinployea* and its relatives. To a certain extent there are similarities with *Phenacohelix* (fig. 11c, e) in general penis shape, ovotestis, and pallial configuration, but there is a clear difference in vas deferens insertion, talon, and terminal female genitalia configurations. Of the extralimital taxa considered here, *Discocharopa* has the most similarities to *Phenacohelix*, but the degree of their relationship remains unknown.

Because only partial anatomical data was recovered, this general discussion substitutes for a formal description.

Originally, only the Kermadec Islands populations and the Tasmanian *D. bassi* (Legrand, 1871) were placed in *Discocharopa*. Subsequently, Iredale (1937a, p. 325) included several additional Australian and Tasmanian species, Cotton (1939, p. 176) described a *Paralaoma* as belonging to this genus, van Benthem Jutting (1951) named *D. microdiscus* from the Celebes, and I (Solem, 1957, 1959a) added Philippine and New Hebridean (fig. 36) taxa. None of the Tasmanian species, *D. vigens* (Legrand, 1871), *D. bassi* (Legrand, 1871), *D. lottah* (Petterd, 1879), or *D. mimosa* (Petterd, 1879), appear to be correctly classified in *Discocharopa*, but generic reallocation is not attempted here. *Discocharopa concinna* (Hedley, 1901) and *D. planorbulina* (Tate, 1896) from Queensland and the Northern Territory of Australia are synonymized with *D. aperta* (Möllerndorff) from the Philippines. The latter is the oldest name and applies to the single species recognized. *Discocharopa wernerii* Solem (1957, pp. 4–6, fig. 2) from Mindanao is totally unrelated to *Discocharopa*. Its original assignment here was a desperation effort to avoid description of a new genus, compounded by an unwillingness to place it in a New Zealand genus when adequate comparative material was lacking.

Combining all described species with *D. aperta* is based upon examination of all types and study of over 300 specimens. This results in recognizing a species with the widest distribution of any endodontoid, extending from the northern Philippines and Java to Central Australia, Kermadec Islands, and the Society Islands. The only approximately equivalent distribution is that shown by *Stenopylis coarctata* (Möllerndorff, 1894), which has almost the same Indonesian and Australian range, but only reaches the Solomon Islands and has not been found in the New Hebrides, Fiji, Kermadec Islands, or Polynesia. Data on this species are summarized by Solem (1957, pp. 8–11, fig. 4). Subsequently it was reported from Bach Long Vi (Nightingale Island) in the Gulf of Tonkin (Saurin, 1960, pp. 7–9, fig. 3, pl. 1; figs. 6a–b, 7) and was mistakenly described as a new species, *Microphyura nightingali*. *Microphyura* is a New Caledonian endemic rhytidid genus whose conchological appearance is convergent with that of *Stenopylis*. Hedley (*in* Tate, 1896, pp. 221–222, fig. C) illustrated the jaw and radula of *Stenopylis*. Tentatively, I (Solem, 1975) classified it in the Helicodiscidae, an otherwise North American complex, and subsequent dissection has confirmed this assignment (Solem, unpublished data).

*Discocharopa* and *Stenopylis* have been collected together on several occasions, and I suspect their ecological requirements are very similar. The method of apertural narrowing is very different, with *Discocharopa* using a single, deeply recessed parietal, whereas *Stenopylis* uses a combination of lip thicken-

ing and internal tubercles (Solem, 1957, p. 11, fig. 4b-c, e).

Differences of *Discocharopa* from other genera are gross in nature. *Microcharopa* from Fiji is most apt to be confused in size but is slightly smaller (mean diameter 1.07 mm.), has strong spiral apical sculpture (fig. 4a-e, p. 13), proportionately larger apical whorls, and more evenly rounded body whorl contours. *Punctum* has a much higher spire, is distinctly smaller, has prominent spiral apical cords and a narrower umbilicus. No Pacific Island Charopidae without prominent apertural barriers average less than 2.00 mm. in diameter, whereas those *Lagivala* and *Vatusila* in the 1.40-1.75 mm. size range have very prominent apertural barriers at or very near the lip edge. Most of these have marked lateral body whorl compression. Of the six Endodontidae averaging less than 2 mm. in diameter, only the Manu'a Group *Minidonta manuaensis* Solem 1976, occurs within the geographic range of *Discocharopa*. That species has more than four whorls, a very narrow umbilicus, H/D ratio over 0.550, and seven prominent apertural barriers. The other species of *Minidonta* are Hawaiian, Mangarevan, and the Bikini Atoll fossil, *M. inexpectans* (Ladd, 1958).

***Discocharopa aperta* (Möllendorff, 1888). Figures 5a-f, 34a-d, 35a-b, 36a-c, 37a-d.**

*Patula aperta* Möllendorff, 1888, Nachr. Bl. deut. Malak. Gesell., 20 (5-6), p. 89—Montalban, Rizal, Luzon, Philippines; Pilsbry, 1892, Man. Conchol., (2) 8, pp. 80-81, pl. 37, figs. 35-37; Möllendorff, 1898, Abhl. Naturf. Ges. Görlitz, 22, p. 88—Luzon, Leyte, Calamianes.

*Endodonta (Charopa) planorbulina* Tate, 1896, Rep. Horn Sci. Exped. Central Australia, (2), p. 187, pl. 17, fig. 3—Palm Creek, Krichauff Range, Northern Territories, Australia.

*Endodonta concinna* Hedley, 1901, Proc. Linn. Soc. New South Wales, 25, p. 729, pl. 48, figs. 1-3—Bundaberg, Queensland, Australia.

*Charopa (Discocharopa) exquisita* Iredale, 1913, Proc. Malacol. Soc. London, 10 (6), pp. 379-380, pl. XVIII, fig. 8—Sunday Island, Kermadec Group.

*Ptychodon celebica* B. Rensch, 1932 (not Sarasin & Sarasin, 1899), Zool. Jahrb., Syst., 63, p. 101—Sumba; B. Rensch, 1935, Sitzber. Gesell. Naturf. Freunde, Berlin, 1935, p. 322—Timor.

*Pyramidula aperta* (Möllendorff), Faustino, 1930, Philippine J. Sci., 42 (1), p. 110.

*Discocharopa planorbulina* (Tate), Iredale, 1937, Australian Zool., 8 (4), p. 325; Iredale, 1937, South Australian Nat., 18 (2), p. 25, pl. 1, fig. 21.

*Discocharopa concinna* (Hedley), Iredale, 1937, Australian Zool., 8 (4), p. 325.

*Charopa exquisita* (Iredale), I. Rensch, 1937, Arch. f. Naturgesch., n. f., 6 (4), pp. 590-591—Malkong-Bach, Weiten Buch and Vunapope, Gazelle Peninsula, New Britain, Bismarck Archipelago.

*Charopa (Discocharopa) microdiscus* van Benthem Jutting, 1951, Basteria, 15 (1-2), pp. 28-29, fig. 1—South Celebes and West Java; van Benthem Jutting, 1952, Treubia, 21 (2), p. 398—West Java; van Benthem Jutting, 1953, *ibid.*, 22 (2), p. 302—Ambon.

*Discocharopa aperta* (Möllendorff), Solem, 1957, Fieldiana: Zoology, 42 (1), pp. 3-4, fig. 1, a-d—Luzon and Catanduanes, Philippine Islands.

*Discocharopa microdiscus* van Benthem Jutting, Solem, 1958, Arch. f. Mollusk., 87 (1-3), p. 21.

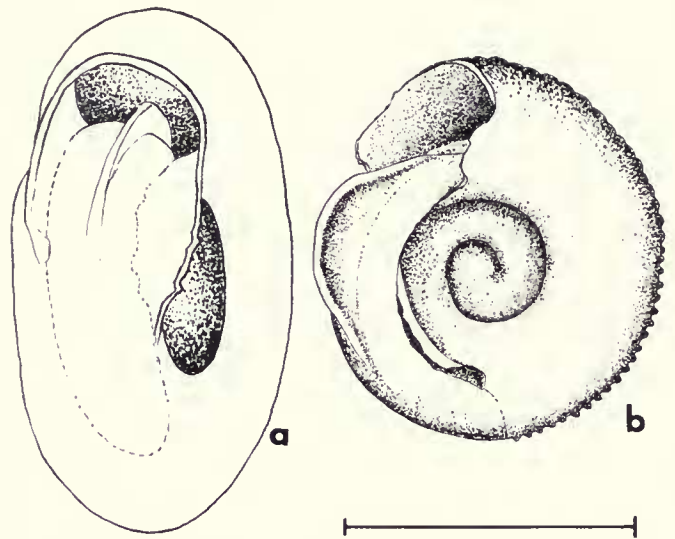


FIG. 35. Parietal barrier variation in *Discocharopa aperta* (Möllendorff): a, Tjamba Pass, near Makassar, Celebes. ZMA; b, Blue Lake, Sunday Island, Kermadec Islands. Paratype of *Charopa exquisita* Iredale, 1913. FMNH 117214. Scale line equals 1 mm. (JC).

*Charopa microdiscus* van Benthem Jutting, 1958, Verh. Naturf. Ges. Basel, 69 (1), p. 106—Sumba, Indonesia.

*Discocharopa planulata* Solem, 1959, Fieldiana: Zoology, 43 (1), pp. 82-83, pl. 32, figs. 1-3—stream drift in Sarakata River Valley, Espiritu Santo, New Hebrides.

**Diagnosis.**—Shell minute, diameter 1.18-1.84 mm. (mean 1.36 mm.), with  $3\frac{1}{2}$ -4 $\frac{1}{4}$  normally coiled whorls. Apex and spire rarely flat, usually slightly to moderately elevated, body whorl descending more rapidly to very strongly deflected (Rurutu, Austral Islands), spire protrusion  $\frac{1}{2}$  to more than  $\frac{1}{4}$  body whorl width, usually about  $\frac{1}{6}$ , H/D ratio 0.341-0.615<sup>2</sup> (mean 0.438). Apical sculpture of radial ribs that on lower portion of apex becomes more crowded, with barely visible spirals. Postnuclear whorls with prominent, narrow, sharply defined, strongly protractively sinuated radial ribs, 77-148 (mean 110.6) on the body whorl, whose interstices usually are 2-4 times their width. Ribs/mm. 18.0-40.4 (mean 26.9). Microsculpture of very fine radial riblets, 3-5 between each pair of major ribs, no secondary spiral sculpture. Umbilicus very widely open, saucer-shaped, regularly decoiling, contained 2.00-3.21 times (mean 2.58) in the diameter, margins rounded. Sutures impressed, whorls strongly rounded above and on basal margin, usually very slightly to slightly compressed laterally above and below evenly rounded periphery. Aperture subcircular, moderately to strongly compressed laterally above periphery, less strongly compressed laterally below periphery, inclined 10°-30° from shell axis. Parietal wall with or without a medial barrier, which, when present, is usually recessed  $\frac{1}{4}$  to more than  $\frac{1}{4}$  whorl and varies from a low cordlike ridge extending  $\frac{3}{16}$  of a whorl to a very high crescentic lamella of up to  $\frac{3}{4}$  aperture height, with gradual anterior and posterior descensions, moderately expanded and weakly serrated medially when very high. Presence or absence on either a populational or individual basis. Color white, with at most a faint yellow tinge.

In having stronger radial than spiral apical sculpture, a very widely open umbilicus, and at most only a single very deeply recessed parietal barrier, *Discocharopa aperta* is immediately differentiated from other species of similar size. Species of *Beilania* and

<sup>2</sup>The only two specimens with H/D ratio greater than 0.500 (0.549, 0.615) are Rurutu examples with greatly deflected body whorls.



*Lagivala* have spiral apical sculpture predominating, more apertural barriers that are near the lip edge (at least for the parietals), and generally much thicker body whorls with less sinuated sculpture. *Microcharopa mimula* is most similar in size and shape, but differs in its very distinctive apical sculpture (fig. 4), lower whorl count, lack of apertural barriers, and proportionately much larger apical whorls.

*Description of Patula aperta*.—Shell minute, with slightly less than 3% normally coiled whorls. Apex flat, spire slightly elevated, body whorl descending a little, H/D ratio 0.443. Apical whorls 1½, sculpture partially eroded, but traces of radial ribbing remaining. Postnuclear whorls with narrow, somewhat irregular radial ribs, eroded over much of the shell. Microsculpture obscured by incrustations and eroding of surface except for faint traces in umbilicus. Sutures deep, whorls strongly rounded above, somewhat flattened laterally above periphery with evenly rounded outer margins. Umbilicus saucer-shaped, regularly decoiling, contained 2.51 times in the diameter, with evenly rounded margins. Color white, with periostracal remnants having a faint yellow tone. Aperture subcircular, slightly flattened laterally above periphery, inclined about 15° from the shell axis. No parietal barrier visible from aperture. Height of lectotype 0.64 mm., diameter 1.45 mm.

*Lectotype*.—Philippine Islands: Luzon, Montalban. SMF 165358.

*Description of Endodonta (Charopa) planorbulina*.—Shell minute, with slightly more than 3% normally coiled whorls. Apex and spire barely protruding, last whorl not descending, H/D ratio 0.400. Apical whorls 1½, surface badly eroded with only faint traces of regularly spaced radial ribbing remaining. Postnuclear whorls with moderately widely spaced, protractively sinuated radial ribs, 91 on the body whorl, whose interstices are 2–3 times their width. Microsculpture mainly eroded, consisting, when visible, of faint radials. Sutures relatively deep, whorls strongly rounded above, slightly flattened laterally above periphery with evenly rounded outer margin. Color white. Umbilicus saucer-shaped, regularly decoiling, contained 2.70 times in the diameter with rounded margins. Aperture subcircular, slightly flattened laterally above periphery, inclined about 10° from shell axis. Height of holotype 0.61 mm., diameter 1.52 mm.

*Holotype*.—Australia: Palm Creek, Krichauff Range, Northern Territories. SAM D.3222.

*Description of Endodonta concinna*.—Shell minute, with 3½ relatively loosely coiled whorls. Apex and spire barely elevated, last half of body whorl descending moderately, H/D ratio 0.445. Apical whorls 1½, sculpture of relatively widely spaced radial ribs with an extremely fine microsculpture of more crowded spiral riblets. Remaining whorls with narrow, relatively crowded, protractively sinuated radial ribs, about 102 on the body whorl, whose interstices are 2–4 times their width. Microsculpture barely visible, consisting of fine radial riblets. Sutures relatively impressed, whorls strongly rounded above, flattened laterally above periphery and partially on basal margin. Color very light yellowish white. Umbilicus saucer-shaped, regularly decoiling, contained 2.81 times in the diameter. Aperture ovate, compressed laterally above periphery and on basal margin, inclined about 15° from the shell axis. Height of lectotype 0.61 mm., diameter 1.48 mm.

*Lectotype*.—Queensland: Bundaberg. AMSC.8970.

*Description of Charopa (Discocharopa) exquisita*.—Shell minute, with 3¼ normally coiled whorls that only slightly increase in width. Apex and spire barely emergent, body whorl descending slightly, H/D ratio 0.450. Apical whorls 1½, first quarter whorl worn smooth, lower sculpture of prominent, narrow radial ribs, more widely spaced above, becoming crowded near end, with microsculpture of very fine spiral ribbing. Remaining whorls with narrow, strongly protractively sinuated lamellar radial ribs, 100 on the body whorl, whose interstices are 3–5 times their width. Microsculpture of very faint

radial riblets. Sutures deeply impressed, whorls evenly rounded. Umbilicus saucer-shaped, broadly opened, regularly decoiling, contained 2.58 times in the diameter. Color light yellow-horn without darker maculations. Aperture circular, flattened laterally above periphery, inclined about 20° from shell axis. Parietal wall with single, very deeply recessed barrier visible through shell. Height of lectotype 0.59 mm., diameter 1.32 mm.

*Lectotype*.—Kermadec Islands: crater slopes northeast of Blue Lake, Sunday Island. Collected under stones by W. R. B. Oliver on October 3, 1908. DMW.

*Description of Charopa (Discocharopa) microdiscus*.—Shell minute, with slightly more than 3% normally coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending a little more rapidly, H/D ratio 0.424. Apical whorls 1½, sculpture of narrow, prominent, moderately widely spaced radial ribs, becoming more crowded near end with a much finer, very inconspicuous microsculpture of spiral ribs. Postnuclear whorls with fine, strongly protractively sinuated lamellar radial ribs, 111 on the body whorl, whose interstices are 2–3 times their width. Microsculpture barely visible under extreme magnification, consisting of very fine radial riblets. Color very faint yellowish white. Sutures deep, whorls strongly rounded above, flattened laterally above and below evenly rounded periphery with slightly flattened columellar margin. Umbilicus very broadly open, saucer-shaped, regularly decoiling, contained 2.25 times in the diameter. Aperture subcircular, flattened laterally above and below periphery, inclined about 15° from the shell axis. No parietal barrier visible from aperture. Height of holotype 0.69 mm., diameter 1.63 mm.

*Holotype*.—South Celebes: hills of Pangkadjene, Makassar. ZMA.

*Range*.—Philippines and Java east through Sumba, Timor, and Biak to the Bismarck Archipelago, New Hebrides, and Fiji, Kermadec Islands, Manu'a Group in Samoa, Rurutu in the Austral Islands, Borabora in the Society Islands, Northern Australia as far south as the MacDonnell Ranges and Northern Victoria, and Bundaberg in coastal Queensland. Probably in most intermediate areas.

*Material*.—Philippine Islands: north Luzon (4 specimens, RSME); Montalban (7 specimens SMF 165358–60, NMWC). Catanduanes (1 specimen, FMNH 57193). Panglao (1 specimen, RSM). Calamianes: Koron (3 specimens, SMF 165361). Mindanao: Samial (5 specimens, SMF 165362). Busuanga (4 specimens, SMF 165363, FMNH 18725). Bulacan: Bayabac (7 specimens, SMF 165364–5).

Java: Koeripan, Buitzenborg (2 specimens, ZMA, collected February 21, 1932, by van Benthem Jutting).

Sumba: Waikarudi (2 specimens, NHB 6092-c); Langgaliru (1 specimen, NHB 6092-d); Kedi (1 specimen, NHB 6092-b); Mau Marru (5 specimens, NHB 6092-a, ZMA).

Ambon (2 specimens, ZMA, collected October 11–13, 1949, by M. A. Lieftinck).

South Celebes: Pangkadjene near Makassar (21 specimens, ZMA, collected May 9 and October 14, 1948, by G. A. Tammes-Bolt); Palopo near Rante Pao, 23 km. from Makale at 700–800 m. elevation (1 specimen, ZMA, collected October 13, 1948, by G. A. Tammes-Bolt); Kalkrotsenlangs Grote, on way from Makale,

near Kalossi at 700–800 m. elevation (4 specimens, ZMA, collected September, 1948, by G. A. Tammes-Bolt).

Timor: Araki-Vlakte (4 specimens, ZMA, collected April 12, 1950, by B. Polak); Niki-Niki (5 specimens, NHB 4169-a); Noilmina (40 specimens, ZMB, FMNH 146025).

Biak: Zuid-Biak Subdistrict (Station G-24) (olim Sorido) (1 specimen, ZMA, collected March 26, 1952).

Aru Islands: Wokan (1 specimen, MSNG).

Queensland: Bundaberg (9 specimens, AMS C.8970, FMNH 117331).

Northern Territory: Palm Creek, Krichauff Range, near Hermannsburg (3 specimens, SAM D.3222); Station WA-130, Cycad Gorge, Palm Creek, Krichauff Range (7 specimens, FMNH 171558); Station WA-113, Glen Helen entrance to Finke Gorge, MacDonnell Ranges (1 specimen, FMNH 182104); Station WA-133, Temple Bar Gap, MacDonnell Ranges (1 specimen, FMNH 182119); Station WA-446, Kathleen Spring, Gill Range (3 specimens, FMNH 200476).

Western Australia: Stations WA-303 and WA-305, 0.5–1.0 km. east of Yammera Gap, Napier Range (2 specimens, FMNH 199179, FMNH 199245); northwest of Stumpy's Well, southwest side Napier Range (1 specimen, WAM 824–76); "The Tunnel," Tunnel Creek, Napier Range (1 specimen, WAM 1758–78); Stations WA-257 and WA-258, Brooking Gorge, Oscar Ranges (9 specimens, FMNH 199491, FMNH 199547); Station WA-255, near Gieke Gorge Ranger station, Gieke Gorge National Park, Oscar Ranges (3 specimens, FMNH 199597); Cave Spring, Bugle Gap, Lawford Ranges (WAM).

New Britain: Vunapope (12 specimens, ZMB, FMNH 146027); Malkong (3 specimens, ZMB).

New Hebrides: Vila, Vate (3 specimens, BMNH 1915.12.31.602, AMS C.15679); Sarakata River, Espiritu Santo (3 specimens, MCZ 186826, FMNH 54904, BPBM 212378).

Kermadec Islands: Sunday Island (34 specimens, AIM, IRB, DMW 12449); under pumice on Mt. Junction (4 specimens, DMW 12424, collected September 18, 1908, by W. R. B. Oliver); under stones on crater slope, northeast of Blue Lake (14 specimens, DMW 12423, FMNH 117214, collected October 3, 1908, by W. R. B. Oliver).

Fiji: Viti Levu: Sigatoka, near base of limestone cliff,  $\frac{1}{2}$ – $1\frac{1}{2}$  miles inland (1 specimen, BPBM 87930, collected July 12, 1928, by H. S. Ladd); Lami Ridge (Station 47), 5 miles west of Suva at 5–150 ft. elevation (2 specimens, BPBM 178489, collected July 24, 1938, by Y. Kondo and C. M. Cooke, Jr.).

Fiji: Lau Archipelago: Yangasa Levu, south end (Station 30), about 150 ft. inland at 40 ft. elevation (17 specimens, BPBM 167137, collected July 26, 1934, by H. S. Ladd); Navutu-I-Loma (1 specimen, BPBM 167102); northeast quarter (Station 28), 150 yd. inland at 100 ft. elevation (3 specimens, BPBM 167017,

collected July 24, 1934, by H. S. Ladd); Namuka (1 specimen, BPBM 166668): Matandolo (Station 2), north-central point of island, 500 ft. inland at 65–75 ft. elevation (6 specimens, BPBM 166614, collected July 7, 1934, by H. S. Ladd); Wangava (4 specimens, BPBM 166994): northeast end (Station 27),  $\frac{1}{4}$  mile inland at 75 ft. elevation (3 specimens, BPBM 166965, collected July 22, 1934, by H. S. Ladd); Karoni (1 specimen, AIM, collected July 4, 1977, by Walter Cernohorsky): slope of peak at about 90 ft. elevation (6 specimens, BPBM 78603, BPBM 78606, collected August 15, 1924, by E. H. Bryan, Jr.); Aiwa: southwest quarter of island (Station 40), 50 yd. inland at 25 ft. elevation (1 specimen, BPBM 167208, collected August 7, 1934, by H. S. Ladd); Nayau: Nauko (Station 43),  $\frac{1}{2}$  mile inland at base of limestone cliff, 250 ft. elevation (3 specimens, BPBM 167230, collected August 13, 1934, by H. S. Ladd); Vanua Mbalavu: between Valika and Mosomo Bay (Station 78), limestone hill about  $\frac{3}{4}$  mile inland at 200–250 ft. elevation (4 specimens, BPBM 179582-3, collected August 9, 1938, by E. C. Zimmerman and Y. Kondo).

Samoa: Aunuu Island off Tutuila: 10 yd. east of lighthouse, 200 yd. inland at 250 ft. elevation (4 specimens, BPBM 83243, collected February 4, 1926, by T. Dranga) (1 specimen, BPBM 171020).

Ta'u: Siufaga (Station 76) (1 specimen, BPBM 171074); Tavalagi Ridge (Station 75),  $\frac{1}{8}$  mile inland at 450 ft. elevation (27 specimens, BPBM 171066, BPBM 171107); Lepuu Cliffs (4 specimens, BPBM 171126). Olosega: Olosega Village (1 specimen ex BPBM 188720).

Society Islands: Borabora, south slope (Station 1093) of Pahio-Temanu ridge, 800 ft. elevation in dirt at cave entrance (1 specimen, BPBM 152396, collected October 13, 1934, by Gessler and St. John).

Austral Islands: Rurutu: Mato Naa, bluff north of Moerai (Station 760), 20–30 yd. inland at 5–15 ft. elevation (6 specimens, BPBM 148292); Mato Arei (Station 775), cliff southeast of Moerai at 50–150 ft. elevation (6 specimens, BPBM 148559, collected August 27, 1934, by Y. Kondo and D. Anderson).

*Remarks.*—Except for collections from river drift or detritus sweepings, *Discocharopa aperta* (Möllerndorff) is represented in collections by very small samples. Partly this results from its small size, but more probably from the secretive habits and actual rarity. Iredale (1913, p. 366) reported that specimens were found under "a piece of black bark," later "on the underside of moss-covered stones deeply imbedded in earth on the side of the cliff," a "few . . . under dead nikau leaves," and "under loose dry pumice stones in the crater." He reported that "Only two or three were found at a time." No other data have been recorded concerning the habits of living specimens.

At different times since 1961, I have been able to examine the types of all described species. Some were restudied a second time in order to check on details overlooked initially or to confirm structures. Despite



the variations outlined below, I conclude that only one species can be recognized. My list of material covers all the references cited above except for that of "*Ptychodon celebica*" from B. Rensch (1932, p. 101; 1935, p. 322). Broken or juvenile examples from these materials were seen in the SMF collection, but were not measured or listed. They are *Discocharopa*, however, and not *Beilania philippinensis* (Semper). Description of several species was caused by the wide geographic range, large shape variation, and the short diagnoses originally presented. I am among the guilty, since *Discocharopa planulata* Solem (1959a) from the New Hebrides is based on rather large and widely umbilicated shells (fig. 36a-c). Previously (Solem, 1957, p. 4) I had

suggested that the Philippine *D. aperta* and Indonesian *D. microdiscus* might be synonymous, but failed to extend this to the other taxa.

Data on size and shape variation are summarized in Table XIII. The growth pattern is such that certain separation of adult from subadult examples is very difficult with fresh material and virtually impossible with worn, dead shells from river drift or detritus. Calculations have been restricted to means and ranges under these circumstances. Despite a certain partial mixture of subadults and adults, there is quite minor variation in size and shape. Specimens from the Bismarck Archipelago are distinctly smaller and have more numerous, crowded radial ribs. Australian

TABLE XIII. - GEOGRAPHIC VARIATION IN DISCOCHAROPA APERTA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER
<u>Montalban, Luzon, Philippines</u>	11	102.0(99-105)	23.7(23.2-24.0)	0.58(0.49-0.66)	1.38(1.27-1.53)
<u>Northern Luzon</u>	5	104.7(100-110)	24.6(24.0-25.4)	0.59(0.53-0.66)	1.31(1.15-1.38)
<u>Sumba and Celebes</u>	12	101.4(78-123)	26.3(21.8-31.3)	0.55(0.42-0.69)	1.27(0.99-1.63)
<u>Timor</u>	25	100.9(77-127)	24.4(18.0-34.7)	0.56(0.48-0.69)	1.34(1.09-1.55)
<u>New Britain, Bismarcks</u>	11	133.0(118-148)	35.3(30.2-40.6)	0.65(0.48-0.67)	1.21(1.07-1.45)
<u>Krichauff Mts., N. Territories, Australia</u>	3	88.3(84-91)	19.7(19.2-20.8)	0.59(0.58-0.61)	1.43(1.38-1.51)
<u>Bundaberg, Queensland, Australia</u>	5	102	21.9	0.63(0.59-0.67)	1.47(1.40-1.56)
<u>New Hebrides</u>	5	127.3(125-131)	29.5(29.2-29.6)	0.54(0.46-0.63)	1.36(1.25-1.43)
<u>Fiji, Lau Group</u>	7	135.7(125-147)	31.1(28.5-35.7)	0.64(0.53-0.74)	1.56(1.32-1.84)
<u>Fiji, Viti Levu</u>	3	140	29.2	0.58(0.46-0.70)	1.39(1.25-1.53)
<u>Samoa</u>	15	114.0(102-128)	28.0(25.4-30.5)	0.64(0.49-0.72)	1.32(1.07-1.45)
<u>Rurutu, Austral Is.</u>	6	109	25.8	0.70(0.63-0.79)	1.37(1.28-1.48)
<u>Borabora, Society Is.</u>	1	--	--	0.64	1.43
<u>Sunday Id., Kermadec Is.</u>	22	103.7(85-123)	25.1(20.9-30.6)	0.57(0.49-0.63)	1.32(1.23-1.41)

	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO	BODY WHORL WIDTH	SP/BWW
Monta.	0.418(0.385-0.476)	3 1/2-(3 1/4-3 3/4)	0.56(0.53-0.65)	2.57(2.40-2.96)	----	-----
N. Luz.	0.452(0.425-0.476)	3 3/8(3 1/8-3 1/2)	0.52(0.43-0.58)	2.53(2.40-2.69)	----	-----
Sumba	0.430(0.396-0.487)	3 1/2-(3 1/8-4)	0.53(0.39-0.72)	2.39(2.22-2.63)	----	-----
Timor	0.419(0.382-0.488)	3 1/2-(3-3 7/8)	0.53(0.39-0.61)	2.57(2.36-2.77)	----	-----
N. Bri.	0.444(0.402-0.466)	3 3/8+(3 1/4-3 5/8)	0.49(0.43-0.59)	2.48(2.38-2.58)	----	-----
Krich.	0.409(0.400-0.417)	3 1/8(3-3 1/4)	0.54(0.51-0.56)	2.66(2.57-2.71)	----	-----
Bunda.	0.428(0.404-0.445)	3 1/2+(3 1/2-3 3/4)	0.55(0.51-0.64)	2.68(2.44-2.81)	----	-----
N. Heb.	0.400(0.341-0.437)	3 1/2(3 1/4-3 5/8)	0.60(0.53-0.66)	2.29(2.16-2.63)	0.38	0.130
Lau	0.410(0.390-0.450)	3 3/4+(3 1/2-4 1/4)	0.72(0.48-0.92)	2.21(2.00-2.76)	0.40(0.35-0.44)	0.178(0.111-0.292)
V. Levu	0.418(0.368-0.457)	3 3/8+(3 1/4-3 5/8)	0.46(0.44-0.48)	3.04(2.81-3.21)	----	-----
Samoa	0.486(0.429-0.524)	3 1/2-(3 1/4-3 5/8)	0.47(0.39-0.61)	2.80(2.59-3.09)	0.39(0.34-0.41)	0.171(0.091-0.286)
Rurutu	0.514(0.444-0.615)	3 5/8(3 3/8-4)	0.51(0.41-0.59)	2.71(2.50-3.12)	0.41(0.38-0.44)	0.208(0.146-0.240)
Borab.	0.448	3 1/2+	0.61	2.35	0.41	0.120
Sunday	0.434(0.390-0.469)	3 1/4+(3-3 1/2)	0.48(0.46-0.56)	2.57(2.42-2.68)	----	-----

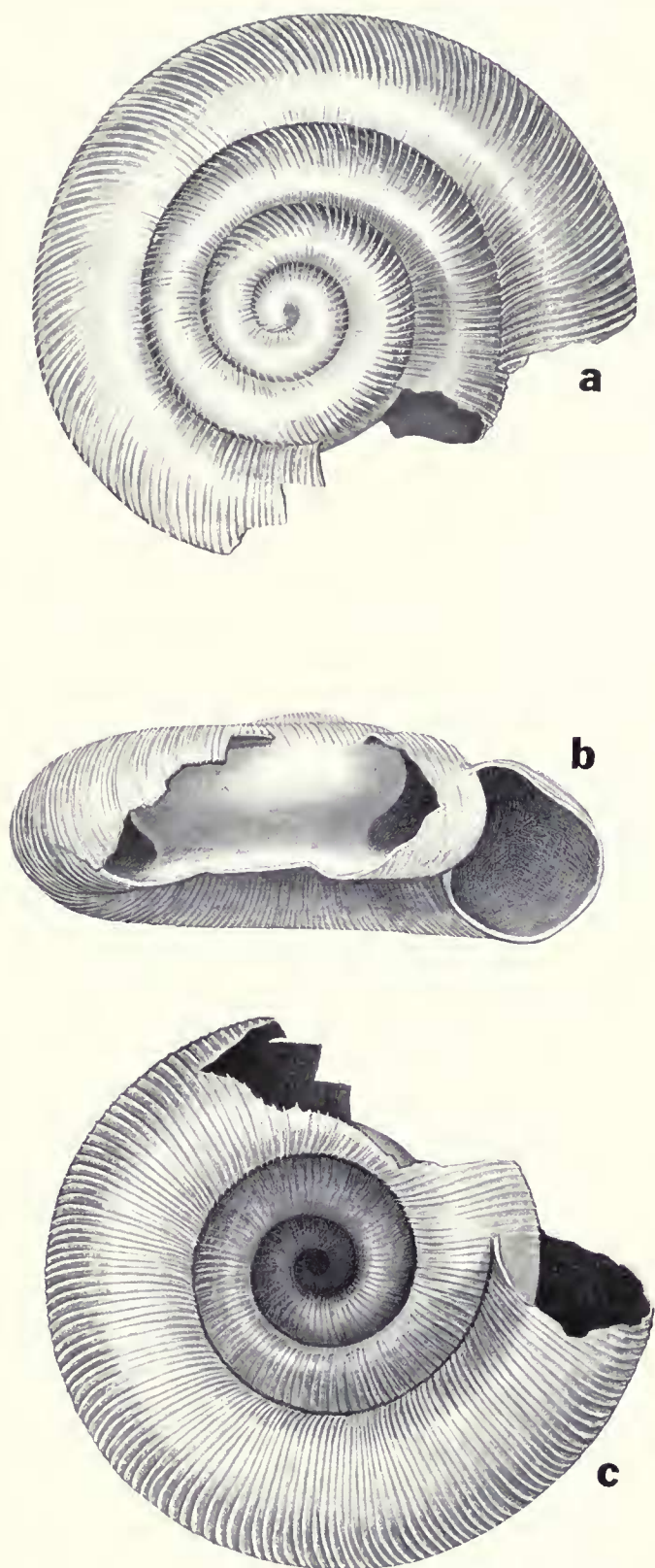


FIG. 36. a-c, *Discocharopa aperta* (Möllendorff) from the New Hebrides. River drift, Sarakata River, Espiritu Santo, New Hebrides. Holotype of *Discocharopa planulata* Solem, 1959. UMMZ 186037. Scale line equals 1 mm. (Solem, 1959a, pl. 32, figs. 1-3). (EJP).

specimens are large and have fewer and more widely spaced radial ribs (fig. 37a-d). Lau Archipelago shells are very large and widely umbilicated, with the New Hebridean shells only slightly smaller (fig. 36a-c). Both have intermediate ribbing frequency and spacing.

Shells from Viti Levu and Samoa are much more narrowly umbilicated. The higher H/D ratio and narrower umbilicus in the Rurutu shells results from drastic deflection of the body whorl. Otherwise, differences are well within the range of statistical error.

Probably more importance can be attached to variation in the parietal barrier. Kermadec shells (fig. 35b) have a very large barrier recessed about one-quarter whorl and usually visible through the shell, but not from the aperture. Rurutu examples have a slightly smaller parietal that was clearly visible from the aperture, as did the single example from the Society Islands. Specimens from the Lau Archipelago had a parietal visible in juveniles, sometimes large and sometimes small, but not visible from the aperture in any adults. No Lau Archipelago adults had a translucent shell, but unless there was deeper recession of the barrier in adults, it should have been visible. No Australian, Samoan, Viti Levu, or New Hebridean shells showed any trace of a parietal.

A number of Samoan shells were sufficiently translucent to allow confirmation of the parietal's absence. Some Philippine specimens had a low to medium parietal, but most showed no trace of a barrier. Most Sumba examples had a large parietal, whereas the Celebes shells (fig. 35a) showed a moderately recessed, rather long barrier that at most extended one-third of the apertural width.

It is obvious from the above paragraphs that variations show a mosaic pattern and that the variables are not correlated in any obvious fashion. Widely umbilicated Celebes shells have a strong parietal, whereas the widely umbilicated New Hebridean specimens lack all trace of a parietal, and the Lau Archipelago examples have a parietal in the juvenile stage but not the adult. Viti Levu examples are narrowly umbilicated and without a parietal barrier.

Material from the island groups covered in this monograph were relatively distinct from each other, but when specimens from extralimital areas were considered, the differences were duplicated. Only one example from Borabora (BPBM 152396) was seen. Although broken and with the sculpture worn, the large parietal, relatively wide umbilicus and rather low spire are very different from the Rurutu shells. These have the spire markedly elevated and a correlated rather tight coiling pattern. In some (BPBM 148559) the body whorl is abruptly deflected, which greatly increases the H/D ratio and narrows the umbilicus. All examples had a parietal visible from the aperture.

Samoan specimens have a raised spire, slightly increased descension of the body whorl, a relatively narrow umbilicus, fairly high H/D ratio, no visible parietal, and, in the few translucent shells, no parietal visible through the shell. A subjective impression is that they have a slightly tighter coiling pattern than do the Fiji specimens.

Lau Archipelago shells, particularly the largest sample (BPBM 167137) from Yangasa Levu, are very widely umbilicated, large shells, with a slight increase



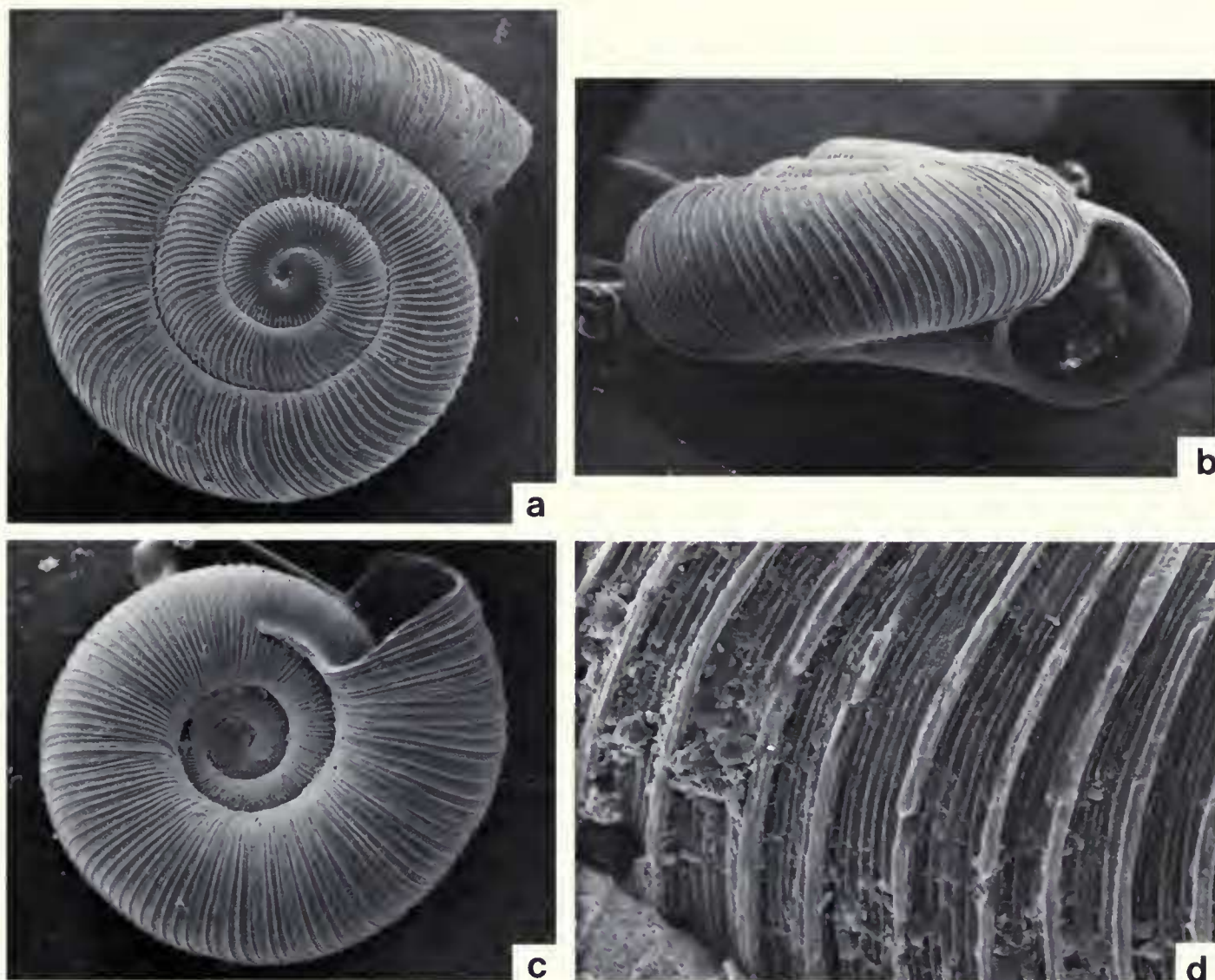


FIG. 37. Australian *Discocaropa aperta* (Möllerndorff). Station WA-113, Glen Helen opening to Finke Gorge, MacDonnell Range, west of Alice Springs, Northern Territory. A. Solem and L. Price! III-12-1974. FMNH 182104: a, top of shell (50 $\times$ ); b, side of shell (54 $\times$ ); c, base of shell (49 $\times$ ); d, sculpture on body whorl (505 $\times$ ).

in whorl count and distinctly more crowded radial ribs on the last portion of the body whorl. Visually they are very similar to the New Hebridean shells. All juveniles showed a large parietal barrier that was readily visible from the aperture. No adults showed any trace of a parietal. The few Viti Levu shells (BPBM 87930, BPBM 178489) are much more narrowly umbilicated and are shaped like the Samoan shells. They lack any trace of a parietal, although at least one is obviously subadult.

Specimens from Rurutu, Samoa, and the Lau Archipelago do have a characteristic appearance and if mixed in a tray could be separated with only slight difficulty. When compared with various Indonesian and Bismarck sets, except for the few Rurutu shells with extreme body whorl deflection, duplicates can be found for each of the Pacific Island types. Nomenclatural recognition would require designation of convergent, isolated geographic races based on use of one or two characters and ignoring those that disagreed, or

recognizing probably polyphyletic subspecies with intermingled mosaic distributions. Neither alternative seems really adequate, particularly since only material from one population has been dissected. Eventual recognition of races or species may be possible, but not until anatomical studies have been made and more data are available concerning the meaning of variation in the parietal barrier.

#### Genus *Sinployea*, new genus

Small to very large Charopidae with  $3\frac{1}{2}$ – $5\frac{1}{2}$  (more in *planospira*) normally to rather tightly coiled whorls. Apex and spire rarely flat, slightly depressed (*lamellicosta*, *tenuicostata*) or barely protruding (*descendens*), normally moderately protruded, sometimes elevated more than  $\frac{1}{4}$  body whorl width (*harveyensis*, *vicaria*, *angularis*, *recurva*). Body whorl descending moderately to drastically (*irregularis*). Apical sculpture normally of 10–12 prominent to fine spiral cords, rarely averaging less than 9 (*tahitiensis*, *allecta*) or more than 13 (*angularis*, *recurva*, *irregularis*), sometimes (*peasei*, *avanaensis*) greatly reduced in prominence. Postnuclear sculpture of extremely fine and crowded (*avanaensis*) to broader and quite widely spaced (*angularis*, *tenuicostata*), usually protractively sinuated ra-



dial ribs, rarely (*recurva*) lost on lower spire and body whorl, sometimes becoming too fine and crowded (*harveyensis*, *irregularis*) or irregular (*rudis*) to count. Microsculpture of fine radial and finer spiral riblets, secondary spiral cording present in  $\frac{2}{3}$  of species. Umbilicus sometimes widely open (*descendens*, *planospira*), rarely (*clista*, *clausa*) closed or barely perforate, normally V-shaped or U-shaped, with last whorl decouling more rapidly, margins rounded. Shell color flammulated, light horn or reddish brown. Sutures deep, channeled only in *proxima*, whorls evenly rounded to strongly compressed laterally above periphery, rarely (*canalis*) with strong lateral compression, periphery rounded, angulated only in *angularis*. Aperture circular to compressedly ovate, inclined  $5^{\circ}$ – $35^{\circ}$  from shell axis. Body color white or with gray on head and ommatophores. Pallial cavity with lobes of kidney subequal in length, generally a strip of lung roof visible between arms of ureter. Genitalia same type as in *Charopa*. Penis length 0.30–0.53 shell diameter, proportionately larger only in *tahitiensis* and *montana*, internally with vergic papilla, muscular collar just below verge tip, and large stimulatory pad near middle portion. Relative size of the penial structures variable.

*Type species.*—*Sinployea peasei*, new species.

Of the other Polynesian genera with typical stimulatory pad, the Viti Levu *Ba* has altered shell form (fig. 74a–c), pallial structures (fig. 75a), and is an experiment in whorl count reduction. The Tongan *Tuimalila* is much larger (table XXXIX), has looser whorl coiling (fig. 78b, e), altered sculpture, and is much larger. *Maafu* (fig. 76a–c) has not been dissected, but its grossly altered shell sculpture and form immediately distinguish it from any *Sinployea*. All of the above groups appear to be specialized derivatives from *Sinployea*. In contrast, the genera with apertural barriers, *Lauopa*, *Vatusila*, *Lagivala*, and *Graeffedon*, probably are much more distantly related. *Graeffedon* (fig. 87c) has a very distinctive epiphallic structure. Only a partial specimen of *Vatusila tongensis* could be dissected (fig. 84a–b). It seems closely related to *Sinployea*.

Intraspecific variation is large enough and similarities between species sufficiently numerous that preparation of a key to all species would have required multiple entries. The more practical solution of preparing keys to taxa from limited segments of the generic range has been adopted. Discussions and either geographic or formal dichotomous keys have been prepared for the species from Society; Cook; Samoan cluster plus Swains Island; Tonga, Ellice, Rotuma, Kusaie in the Carolines, and Saipan in the Marianas; Fiji; and Melanesia (New Hebrides, Solomon Islands, Bismarck Archipelago). In the individual species discussions, cross-references are made to morphologically similar forms from other areas, but the main emphasis is on differentiating taxa from their sympatric or neighboring species.

Some general discussion of variation patterns is presented here, although *Sinployea* is a relatively uniform group in terms of structure.

*Sinployea* has the widest geographic range and greatest number of species recorded for any Polynesian endodontoid genus. I discuss 49 named species-level units below and mention two additional taxa represented by material that is inadequate for description.

Unquestionably, additional species remain to be discovered. Further collections in Tonga, Fiji, Melanesia, and probably on Tahiti should be especially productive. Dissection has confirmed placement of the New Hebridean *S. euryomphala* and the Caroline Island *S. kusaieana* in this genus, but inclusion of the Solomon Island and Bismarck Archipelago species might not be correct. None of them have been dissected. A record from Saipan in the Marianas is questionable. It is possible that *Sinployea* occurs in New Guinea or even Wallacea, since *Pilsbrycharopa kobelti* (Böttger) and *P. brunnescens* (Möllendorff) might be classified in *Sinployea*. Without dissection, their position will remain uncertain. Similarly, some of the New Caledonian species listed in *Andrefrancia* by Solem (1961, pp. 454–463) possibly might be *Sinployea*, although I consider this unlikely, since several dissected *Andrefrancia* have distinctive anatomy. Determination of the exact western distributional limits is beyond the scope of this study and would require collection of additional preserved material.

The great Polynesian distribution of *Sinployea* probably can be explained on the basis of ecology. Many species are semiarboreal in habitat, ascending trees to at least 15 ft., and specimens have been found frequently in leaf axils or attached to loose bark on stilt roots. The opportunity for rare accidental transport during a severe storm is infinitely greater for a species on loose bark than for one in the dense ground litter. Correlated with this habitat difference is the development of gray markings on the ommatophores, head, neck, and sometimes mantle edge in those species that have been found on trees. No trace of gray coloration is seen on those species living only in ground litter or under logs and stones. All of the Society Islands and Cook Island species collected alive in this century show the darker markings. The condition in many Rarotongan species collected on the ground by Garrett, but not found since the 1880s, is unknown. Of the Samoan species for which soft parts are known, only the Swains Island *S. intermedia* lacks gray coloration. The atoll environment with its thinner vegetation cover may have caused this species to become a litter dweller. In contrast, the Caroline Island *S. kusaieana*, Fijian *S. inermis*, *S. adposita*, and *S. irregularis* plus the New Hebridean *S. euryomphala* lack all traces of gray coloration and have been recorded only from the ground stratum. Two Lau Archipelago species in particular may be semiarboreal, but they are known only from empty shells (*S. recurva*, *S. angularis*).

Presently available data suggest that there are two main centers of speciation, Lau Archipelago (six species) and Rarotonga (11 species). In both areas there is evidence of a radiation encompassing both semiarboreal and ground stratum niches. It is quite possible (p. 97) that the Rarotonga litter species are extinct, but I suspect that the Lau Archipelago habitats may be less disturbed. Secondary centers of speciation are found in Samoa (five species) and Tahiti (six species).



Elsewhere, only single species on several islands (Tonga) or separate species on individual islands (Solomons) have been recorded. On Tahiti, only one species has been collected at a station, and on Rarotonga, fragmentary data from recent collecting and records in Garrett (1881) suggest that most, if not all, of the 11 *Sinployea* species were geographically isolated. In Samoa and the Lau Archipelago there is ample evidence of rather extensive sympatry. The above speciation pattern suggests a group of relatively recent arrival that is well adapted for rare accidental transport over great distances, but on particular islands tends to break up into geographic isolates.

In several cases it was possible to dissect sympatric species. In other situations I could study allopatric species populations from only a few hundred yards apart. In each situation there have been shifts in size and/or relative development of the functioning penial elements (verge, muscle collar, and stimulatory pad) that probably serve to enable species recognition and to maintain species isolation. Details of variation in each situation are given in the discussion of Tahitian species (p. 85), Cook Island (p. 95), Samoan (p. 118), and Fijian (p. 147) taxa. Except for these situations of sympatry or almost certain contact between species, I found only slight anatomical differentiation. Variations in whorl count and body whorl capacity affect the relative proportions of the kidney and whether or not a strip of lung roof is visible between the ureter arms. Neither available time nor available material was sufficient to make detailed comparisons of genital proportions. No obvious differences were noted. Although penis length ranged from 0.8–2.2 mm., when allowance is made for differences in adult size by calculating the ratio of mean penis length/mean shell diameter of dissected specimens (table XIV), obviously there is relatively minor variation. Fourteen of 21 dissected *Sinployea* have a PL/ $\bar{X}$ D ratio between 0.35 and 0.47. I consider it significant that departures from this pattern are shown on the opposite ends of distribution. The New Hebridean *S. euryomphala* (Solem), Fijian *S. irregularis* (Garrett), and Society Island *S. neglecta* have small penes, with a ratio of 0.30–0.31. In contrast, two Tahitian species found in close proximity have proportionately very large penes, with ratios of 0.61 and 0.66. Selection pressure for change would occur only where species came into contact or were sympatric, so that the stable genital pattern is not unexpected. The apparent correlation between white body color-litter dweller, gray head and ommatophores-tree trunk habitat was mentioned above.

Conchological patterns of variation are somewhat more extensive, but appear mosaic in nature rather than geographic. Although the range of variation in most measured characters is rather large, the average pattern is relatively conservative. Table XV summarizes mean measurements, giving the minimum, 1st quartile, median, 3rd quartile, and maximum means for 50 taxa (all described material and the Borabora

TABLE XIV. — RATIO OF PENIS LENGTH TO SHELL DIAMETER IN *SINPLOYEA*.

Species	Penis length in mm.	$\bar{X}$ Shell Diameter	PL/D
<i>tahitiensis</i>	2.2–2.4	3.50	0.66
<i>lamellicosta</i>	1.4–1.5	3.25	0.45
<i>modicella</i>	1.0–1.1	3.35	0.31
<i>neglecta</i>	1.4–1.6	2.83	0.53
<i>montana</i>	1.4–1.65	2.50	0.61
<i>atiensis</i>	1.1–1.3	2.70	0.44
<i>andrewi</i>	1.1–1.3	2.95	0.41
<i>peasei</i>	1.1–1.3	3.15	0.38
<i>avanaensis</i>	1.4–1.6	3.21	0.47
<i>clista</i>	1.2	2.53	0.47
<i>aunuana</i>	1.0	2.76	0.36
<i>allecta allecta</i>	1.3–1.5	3.13	0.45
<i>intermedia</i>	1.2–1.6	3.49	0.40
<i>complementaria</i>	1.9–2.2	4.92	0.42
<i>vicaria vicaria</i>	1.3	2.86	0.45
<i>kusaieana</i>	1.0	2.60	0.38
<i>inermis inermis</i>	0.8–1.0	2.60	0.35
<i>i.lakembana</i>	0.8–1.0	2.36	0.38
<i>adposita</i>	1.65	3.29	0.50
<i>irregularis</i>	0.8–1.0	2.87	0.31
<i>euryomphala</i>	0.8	2.64	0.30

adult). For the primary measurements of height, diameter, whorls, and rib count, the 2nd and 3rd quartiles cover from 12%–30% of the total range. Only a few species are strikingly distinctive in size or shape, most are very similar.

Four of the seven smallest species were from the Solomons and Bismarcks, *S. nissani*, *S. kuntzi*, *S. descendens*, and *S. novopommerana*. The other three were *S. ellicensis nukulaelaeana* from Nukulaelae, El-

TABLE XV. — MEAN SPECIES MEASUREMENTS IN *SINPLOYEA*.

	MINIMUM	1ST QUARTILE	MEDIAN	3RD QUARTILE	MAXIMUM
Shell Height in mm.	1.00	1.38	1.55	1.77	2.55
Shell Diameter in mm.	2.08	2.50	2.84	3.35	4.92
H/D Ratio	0.463	0.505	0.538	0.573	0.625
Whorl Count	3 1/2	3 7/8+	4 1/8–	4 3/8–	6 5/8
Diameter/Umbilical Width Ratio	2.73	3.69	4.29	4.99	CLOSED
Ribs on Body Whorl <sup>1</sup>	38.0	77.1	92.5	112.2	225.8
Ribs/mm. on Body Whorl <sup>1</sup>	3.35	8.04	10.8	12.2	21.0
Apical Cords	8.60	9.40	10.2	11.8	18.5

1. Four species have reduced ribbing and were omitted from this table.

lice Islands, *S. godeffroyana* from Viti Levu, and the very modified *S. angularis* from Namuka, Lau Archipelago. The largest species is the Upolu Island *S. complementaria*, with nine of the 11 Rarotongan species comprising the other species averaging more than 3.60 mm. in mean diameter. Concentration of the smaller species in Melanesia may indicate competition from terrestrial helicarionids in the 2.5–3.5 mm. size range, whereas the development of larger *Sinployea* on Rarotonga may be the result of that island lacking terrestrial helicarionids. Because the Rarotongan radiation of *Sinployea* probably is extinct, fieldwork to check these possibilities may be 50 years too late.

Height is closely correlated with diameter in terms of large and small species, although H/D ratio diverges in special circumstances. The great increase in whorl count found in *S. planospira* (fig. 46d) has resulted in a lowered H/D ratio, whereas the flat spire, wide umbilicus, and slightly increased whorl count in *S. canalis* (fig. 49a–c) combine to reduce the H/D ratio. In contrast, the nearly closed umbilicus, strongly elevated spire, and thicker body whorl of the Samoan *S. clausa* (fig. 51d–f) give it the highest H/D ratio in the genus. Only the Tahitian *S. montana*, with a slightly more open umbilicus, equally protruded spire, but more sharply deflected body whorl, is similar in H/D ratio (fig. 41a–c). The Viti Levu *S. irregularis* has a flat or only slightly elevated spire, but a high H/D ratio is produced solely by an often drastic deflection of most or all of the body whorl (fig. 65d–f).

Whorl count is a much less variable character. Ignoring *S. nissani* and *S. montana*, for which only subadult or barely adult material was available, and *S. planospira* (fig. 46d), which is characterized by an abnormally high whorl count, mean whorls range from 3¾– to 5–. Of these, only five of the very largest species average more than 4½ whorls. There are no species I can cite as being experiments in whorl count reduction, whereas only *S. planospira* shows clear evidence of whorl increase. Its mean whorl count of 6½ includes a juvenile shell and is thus quite conservative, yet this species averages 1½ whorls more than any other *Sinployea*.

Relative umbilical width, as measured by the D/U ratio, is determined by the pattern of coiling, number of whorls, body whorl contour, and body whorl descension. Those with wide, cup-shaped umbilici are found in the Bismarcks (*S. novopommerana*, fig. 73c), Rarotonga (*S. canalis*, fig. 49c; *S. planospira*, fig. 46f), Ellice Islands (*S. pseudovicaria*, fig. 61c), whereas the very narrowly umbilicated forms are concentrated in Samoa (all the small species) and Lau (*S. angularis*, fig. 64f; *S. recurva*, fig. 64c; *S. adposita*, fig. 69f). I do not know the reason for this.

Whorl contour is relatively stable, with the channeled suture of *S. proxima* (fig. 46a), strong lateral compression in *S. canalis* (fig. 49b), weak supra-peripheral sulcus in *S. rudis* (fig. 47e) and *S. irregularis* (fig. 65e), and angulated periphery in *S. an-*

*gularis* (fig. 64e) providing the only major alterations. Most species vary in the narrow range from an evenly rounded periphery, as in *S. ellicensis* (fig. 62b) and *S. vicaria* (fig. 58b), to taxa with rather prominent lateral compression above the rounded periphery, such as *S. recurva* (fig. 64b). When specimens are compared directly, such minor differences are obvious, but no quantification of these changes was attempted.

Shell ornamentation is relatively complex and the variations numerous. In several species no counts of major radial ribs were possible. The Rarotongan *S. rudis* (fig. 47d) and the Lau Archipelago *S. recurva* (fig. 64a) have widely spaced major radial ribs on the upper spire that become reduced to absent by the body whorl. In contrast, the Rarotongan *S. harveyensis* (fig. 48a–b) and Viti Levu *S. irregularis* (fig. 65d–e) have the major ribs become so fine and crowded on the body whorl that differentiation of ribs and growth irregularities becomes impossible. Specimens with few radial ribs include the very small *S. angularis* (fig. 64e) and *S. inermis lakembana* (fig. 66e), the very large *S. tenuicostata* (fig. 50d), and the larger than average *S. adposita* (fig. 69e) and *S. lamellicosta* (fig. 40a). By far the greatest number of ribs, mean 225.8, is found in *S. avanaensis* (fig. 45e) from Rarotonga. Of the smaller- to medium-sized species, only the Fijian *S. godeffroyana* (fig. 69a) and Lau Archipelago *S. navutuensis* (fig. 68e) have actual rib counts equaling some of the larger Rarotongan shells. The latter three species have by far the highest ribs/mm. index, whereas *S. adposita* and *S. tenuicostata* have the most widely spaced ribs. The number of microradial riblets varies with the rib spacing and actual sculpture size. Development or loss of secondary spiral cording and relative spacing of the cording showed no consistent pattern that I could relate to size or major sculpture.

Apical cording is variable in prominence; the contrast between the large cords in *S. modicella* (fig. 1a–b) and the faint ones in *S. peasei* (fig. 2a–b) indicate the extent of variation. Actual numbers of cords vary from a mean of 8.6 in the Samoan *S. allecta allecta* to a high of 18.5 in the Viti Levu *S. irregularis*. There is no simple correlation between the number of cords and their relative prominence, because the cord spacing is an additional variable factor. It was not practical to prepare scanning electron microscope photographs of more than a few species. The apical cording is too fine for accurate measurement with a dissecting microscope, and the relief is too great for effective study with a compound microscope. Thus, no detailed analysis of apical sculpture spacing and cord width was possible. Those species averaging 8.6–9.0 apical cords were *S. allecta allecta* from Samoa, *S. tahitiensis* from Tahiti, *S. decorticata* from Rarotonga, *S. inermis* from Lau, and *S. princei* from Taveuni. Those with an enlarged number of apical cords are clustered geographically. The Society Island *S. montana*, *S. lamellicosta*, and *S. neglecta* average 12.5–13.0 cords, whereas the Lau Archipelago *S. adposita*, *S. inermis lakembana*, *S. an-*



*gularis*, and *S. recurva* average 13.0–15.9 apical cords. The presence of both low and high counts in Lau and Fiji emphasizes the complexity of speciation patterns in that area.

#### SOCIETY ISLAND *Sinployea*

It is rather surprising that no species are known from Tahaa, Raiatea, or Maupiti. Suitable habitats were investigated by both Garrett and members of the Mangarevan Expedition. Only one specimen, too worn to merit description, has been found on Borabora. Possibly *Sinployea* does not live on Maupiti or the Tahaa-Raiatea complex. Because the Society Islands represent the eastern limit of distribution for *Sinployea*, patchiness of occurrence would not be unexpected.

Single species are found on Huahine and Moorea; three species, on Tahiti. Because upland collecting on Tahiti has been limited to two partial transects on Mt. Aorai and Mt. Orofena, additional taxa may be found later. *Sinployea neglecta* (fig. 41d–f) from Huahine comes the closest of any species in the genus to being average in characteristics. Its mean measurements (table XVI) depart from the median *Sinployea* figures (table XV) only in having a few more crowded major radial ribs, more spiral apical cords, and a slightly reduced number of microradial riblets. *Sinployea modicella* (fig. 38a–c) from Moorea is much larger, more widely umbilicated, and averages fewer apical cords. There is also a difference in penial size, with *S. neglecta* having a penis length of 1.4–1.6 mm. (53% of shell diameter, which averages 2.83 mm.) and *S. modicella* having a penis length of 1.0–1.1 mm. (31.4% of shell diameter, which averages 3.35 mm.).

All three Tahitian species were collected by the Mangarevan Expedition during the Mt. Aorai transect

of the malacological assistants. None were taken during the Mt. Orofena journey by the expedition botanists and entomologist. *Sinployea tahitiensis* occurred in sparse numbers at several stations from 1,400–6,300 ft. elevation and in Fautaua Valley at 250 m. elevation. *Sinployea montana* was found at Station 866, a valley to the west of the Aorai Trail at 6,000 ft. elevation; *S. lamellicosta*, at Station 870, a valley west of the Aorai Trail at 5,000 ft. elevation. Possibly the latter two were collected in the same valley, but obviously at different elevations.

*Sinployea montana* (fig. 41a–c) is a very small, elevated species with quite narrow umbilicus and rather widely spaced radial ribs. *Sinployea lamellicosta* (fig. 40a–c) has a flat or slightly depressed spire, many apical spiral cords, a wide umbilicus, and very widely spaced radial ribs. *Sinployea tahitiensis* (fig. 38d–f) is fairly large, has a slightly protruded spire, fewer apical cords, more whorls, and a thicker body whorl. Penial differences are marked. *Sinployea tahitiensis* has a penis length of 2.2–2.4 mm. (65.8% of shell diameter), and the penis shows no particular modifications. In *S. montana* the penis length of 1.4–1.65 mm. is only 61% of shell diameter, and the vergic papilla is very large with the muscular collar reduced in size. *Sinployea lamellicosta* has a penis length of 1.4–1.5 mm., or 44.6% of shell diameter, and the stimulatory pad is greatly enlarged (fig. 39h). Thus *S. tahitiensis* is differentiated by penis size, whereas *S. lamellicosta* and *S. montana* have penes of the same size, but in the former there is enlargement of the vergic papilla and in the latter, enlargement of the stimulatory pad. If the latter two species do have a zone of sympatry, probably the changes in penial structure serve to enforce species isolation. Further collecting is needed in the mountains of Tahiti in order to establish the ecological re-

TABLE XVI. — RANGE OF VARIATION IN SOCIETY ISLAND *SINPLOYEA*.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<i>modicella</i> (Ferussac)	399	112.9(89–145)	10.82(8.59–12.21)	1.72(1.35–2.04)	3.35(2.99–3.68)	0.514(0.406–0.598)
<i>tahitiensis</i>	23	60.7(44–71)	5.86(4.67–8.37)	1.75(1.39–2.09)	3.50(2.98–4.04)	0.498(0.428–0.541)
<i>lamellicosta</i> (Garrett)	19	52.4(43–71)	5.44(4.03–7.91)	1.58(1.35–1.74)	3.25(2.78–3.55)	0.487(0.454–0.521)
<i>montana</i>	3	63.0(57–69)	8.04(7.43–8.65)	1.56(1.52–1.59)	2.50(2.45–2.55)	0.623(0.622–0.623)
<i>neglecta</i>	172	108.6(71–143)	12.23(8.84–16.87)	1.51(1.28–1.81)	2.83(2.57–3.26)	0.536(0.441–0.632)
Borabora sp.	1	126	14.14	1.55	2.86	0.540

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW
<i>modic.</i>	4 1/4+(4–4 5/8)	0.96(0.72–1.22)	3.48(2.95–4.28)	9.20(7–13)	0.17(0.07–0.23)	1.01(0.89–1.12)	0.166(0.074–0.226)
<i>tahit.</i>	4 3/8–(4–4 5/8)	0.95(0.66–1.12)	3.68(3.38–4.50)	8.92(6–11)	0.10(0.07–0.13)	1.02(0.95–1.05)	0.104(0.091–0.133)
<i>lamel.</i>	4+(3 3/4–4 3/8)	0.99(0.74–1.22)	3.26(2.89–3.87)	12.50(10–16)	FLAT	0.86(0.72–0.99)	FLAT OR DEPRESSED
<i>monta.</i>	3 5/8+(3 5/8–3 3/4)	0.36(0.30–0.43)	7.24(5.93–8.55)	13	0.15(0.13–0.16)	0.85(0.84–0.86)	0.226(0.220–0.231)
<i>negle.</i>	4 (3 5/8–4 1/4)	0.65(0.53–0.95)	4.39(3.21–5.00)	12.46(10–15)	0.14(0.10–0.23)	0.78(0.72–0.86)	0.180(0.115–0.275)
Borab.	4	0.69	4.14	WORN	0.23	0.89	0.222

relationships and geographical ranges of these species.

Despite the size and shape differences, the Society Island species share a characteristic appearance of very thin major ribs with periostracal lamellar extensions. Most species from other island groups have distinctively lower and broader radial ribs. Secondary spiral cording is absent in *S. montana*, present only on the spire in *S. modicella*, and moderately to strongly developed in the other species. Typical flammulated color patterning is seen in all but *S. montana* and *S. tahitiensis*, which have monochrome shell color. All species show a light to dark gray coloration on the head and neck. *Sinployea modicella* and *S. tahitiensis* have been collected on tree trunks or in axils of low trees, plus the usual log and under stone habitats. *Sinployea neglecta* was found only in the ground stratum, but at these stations no special investigation was made of arboreal habitats.

Because most species are geographically isolated, no formal key has been prepared. The following synopsis provides quick identification of known taxa:

- Moorea: *S. modicella* (Férussac, 1840)
- Huahine: *S. neglecta*, new species
- Borabora: *Sinployea* sp. (probably new)
- Tahiti: *S. montana*, new species (diameter less than 2.75 mm., D/U ratio more than 5.00, H/D ratio more than 0.600)
- S. tahitiensis*, new species (spire elevated, about 9 spiral apical cords, H/D ratio less than 0.550)
- S. lamellicosta* (Garrett, 1884) (spire flat or depressed, about 12.5 spiral apical cords, H/D ratio less than 0.550)

Discovery of additional species is very probable.

***Sinployea modicella* (Férussac, in Deshayes, 1840),  
Figures 1a–e, 38a–c, 39a–b.**

*Helix modicella* Férussac, 1840, Hist. Nat. Moll. terr. fluv., 1, pl. 86, fig. 3; Deshayes, 1850, Hist. Nat. Moll. terr. fluv., 1, pp. 90–91—"sur les hautes montagnes, Taiti" (=Tahiti, Society Islands); Pfeiffer, 1853, Monog. helic. viv., 3, p. 92; Pfeiffer, 1859, Monog. helic. viv., 4, p. 86; Pfeiffer, 1876, Monog. helic. viv., 7, p. 149.

*Pitya modicella* (Férussac), Pease, 1871, Proc. Zool. Soc. London, 1871, p. 474.

*Patula modicella* (Férussac), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93—Huahine (?), Society Islands; Garrett, 1884, J. Acad. Nat. Sci., Philadelphia, 9 (1), pp. 28–29—partly.

*Helix (Patula) modicella* Férussac, Tryon, 1887, Man. Conchol., (2) 3, p. 38, pl. 8, figs. 28–30.

*Endodonta (Charopa) modicella* (Férussac), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

**Diagnosis.**—Shell larger than average, diameter 2.99–3.68 mm. (mean 3.35 mm.), with 4–4½ normally coiled whorls. Apex and spire slightly to moderately and evenly elevated, last whorl usually descending more to sharply more rapidly, spire protrusion about ½ body whorl width, H/D ratio 0.406–0.598 (mean 0.514). Apical sculpture of 7–13 (mean 9.2) prominent spiral cords. Postnuclear sculpture of narrow, prominent, numerous, protractively sinuated radial ribs, 89–145 (mean 112.9) on the body whorl, whose interstices

are 2–5 times their width. Ribs/mm. 8.59–12.21 (mean 10.82). Microsculpture of fine radial riblets, 3–7 between each pair of major ribs, very fine and crowded spiral riblets, plus weak secondary spiral cording on spire that fades out on body whorl. Umbilicus widely open, V-shaped, last whorl decoiling more rapidly, contained 2.95–4.28 times (mean 3.48) in the diameter, margins rounded. Whorl contours and apertural features without marked change from average pattern.

*Sinployea modicella* (fig. 38a–c) is most similar to *S. neglecta* (fig. 41d–f) from Huahine and *S. tahitiensis* (fig. 38d–f) from Tahiti. The former is distinctly smaller, has a narrower umbilicus, more and finer apical cords, and distinctly more prominent secondary spiral cording. *Sinployea tahitiensis* has half as many radial ribs and many more microradial riblets. No extralimital species are close in size and shape.

**Description of figured specimen.**—Shell larger than average, with 4 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending much more rapidly, H/D ratio 0.480. Apical whorls 1¾, sculpture of 13 narrow spiral ribs. Postnuclear whorls with narrow, prominent, protractively sinuated radial ribs, 107 on the body whorl, whose interstices are 2–5 times their width. Microsculpture of fine radial riblets, 3–7 between each pair of major ribs, crossed by very fine and crowded spiral riblets, plus fine secondary spiral cording equal in size to microradials on spire that become weak to absent on body whorl. Sutures deep, whorls strongly rounded above, flattened laterally above periphery and somewhat flattened on basal margin, with evenly rounded outer margin. Color light reddish horn, wide slightly darker flammulations visible above periphery. Umbilicus widely open, V-shaped, last whorl decoiling more rapidly, contained 3.63 times in the diameter, margins rounded. Aperture ovate, strongly flattened laterally above periphery, somewhat flattened on basal margin, inclined about 25° from shell axis. Height 1.55 mm., diameter 3.22 mm.

**Range.**—Moorea, Society Islands.

**Material.**—Moorea: Opunohu Valley on tree trunks under bark (15 specimens, BPBM 89709); Faatoai Valley, 1¼ miles inland (Stations 886, 893, 896, 900) at 150–300 ft. elevation under dead logs and leaves or on trunk of *hau* (335 specimens, BPBM 150331–4, BPBM 150375–9, BPBM 150416–21, BPBM 150473–4); Maramu Valley, 1½–1¾ miles inland (Stations 919, 922) at 50–400 ft. elevation under logs and dead leaves (30 specimens, BPBM 150710–4, BPBM 150754); Tepatu Valley (Stations 927, 929) at 50–800 ft. elevation (7 specimens, BPBM 150872, BPBM 150895–6); Station 478, above Rotonui, Belvidere Outlook, Uponohu Bay (1 specimen, FMNH 201054). "Tahiti" (12 specimens, FMNH 46531, RSM).

**Remarks.**—The taxon *Helix modicella* has been used as a catchall for the small, barrier-free endodontoids of Polynesia and Fiji. In the absence of precise measurements and with the availability of only fragmentary material, such a usage is understandable. Unfortunately, it is difficult to fix the identity of this name. No type material could be located in Paris at the time of my study trips. All material collected on Tahiti in recent years differs from specimens in older collections that were labeled "Tahiti." These shells agree more with the populations from lowland Moorea collected by the Mangarevan Expedition. The type figures have proportions that fall within the range of Moorean material, since the drawing is 9.4 mm. high, 18.5 mm.



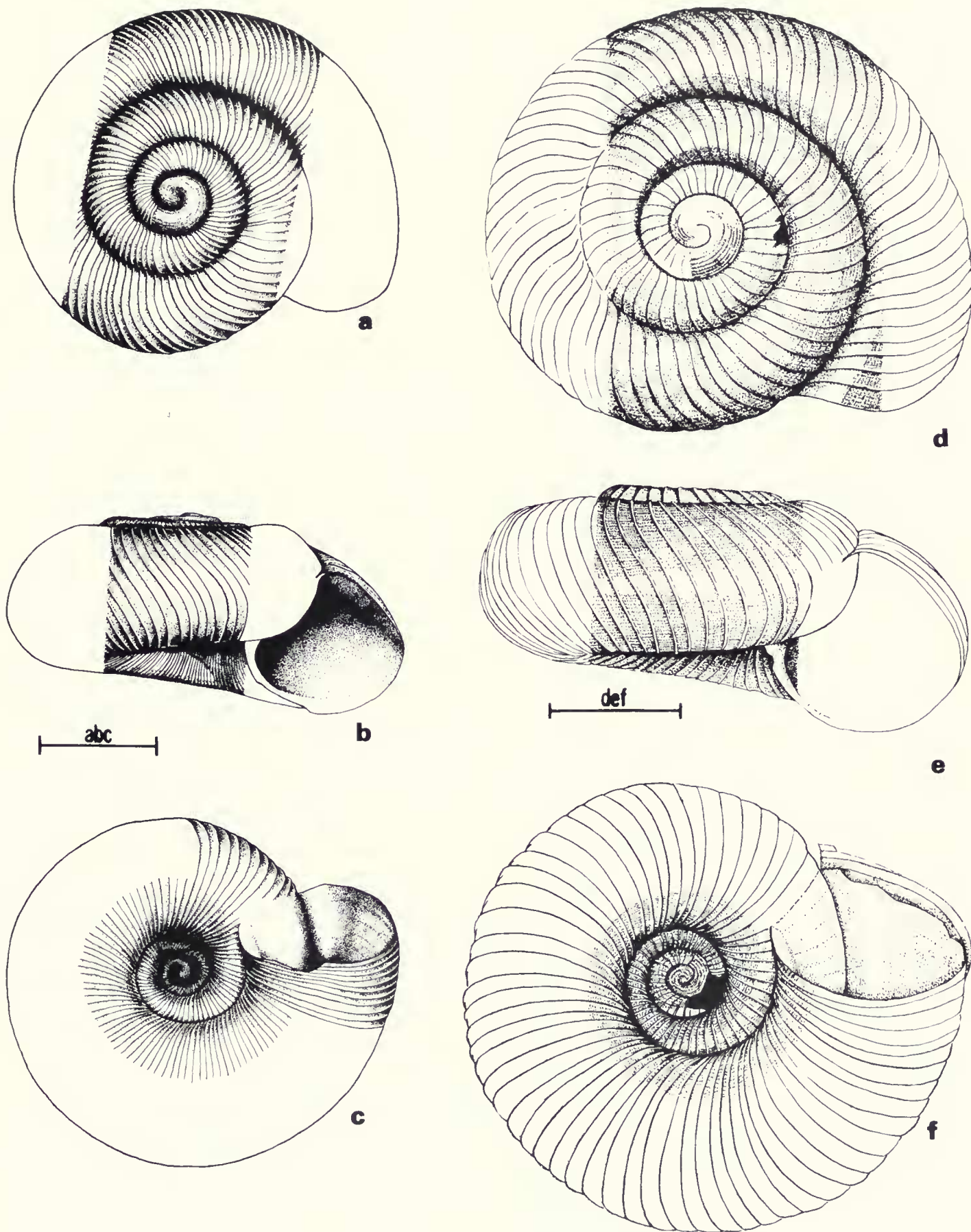


FIG. 38. a-c, *Sinployea modicella* (Férussac). "Tahiti," Society Islands. FMNH 155940. d-f, *Sinployea tahitiensis*, new species. Station 863, Mt. Aorai, 4,700-5,000 ft., Tahiti, Society Islands. Holotype. BPBM 142072. Scale lines equal 1 mm. (SH).

in diameter, with  $4\frac{1}{4}$  whorls, H/D ratio 0.509, D/U ratio 4.02 and about 107 ribs on the body whorl.

Because material from old collections agrees with the Moorean shells, I have no hesitation in restricting the type locality to Moorea. The figured specimen is labeled as coming from "Tahiti" and originating in a collection formed during the middle 1800s. Possibly it is part of the type set, but there is no evidence concerning this. In 1981, the Ecole National Supérieure des Mines deposited material from the Deshayes collection in the Museum National d'Histoire Naturelle, Paris. Included were two lots of *Helix modicella* from "Tahiti." There were 8 and 11 shells glued to strips of cardboard. Through the courtesy of Dr. Simon Tilletier, it was possible to examine these specimens. The smaller lot agrees better in color and sculpture with the figured shell (fig. 38a–c) than the larger lot, but may not be conspecific. The latter specimens are much more brightly colored than the former and have more widely spaced sculpture. Almost certainly they are one of the other Society Island species. Without dismounting and extensive cleaning of each shell, determination of their species identity will not be possible. I have not chosen a lectotype or neotype. I suspect that the material from the Deshayes collection was obtained subsequent to illustration of the original monochromatic specimen. The name *Helix modicella* Ferussac, 1840, is applied to the lowland Moorean populations on the basis of the original illustration.

Variation in local populations is summarized in Table XVII. All these samples were taken between 50 and 800 ft. elevation. Size and shape are practically identical, with only umbilical width varying significantly. Shells from Maramu Valley (Station 919) have a distinctly narrower umbilicus than those from Faatoai Valley (Stations 893, 896), with the small sample from Tepatu Valley (Station 927) intermediate in width. Although the difference between shells from Station 896 and Station 919 is statistically significant, with 24 degrees of freedom,  $t = 4.9127$ , I doubt that there is any systematic difference.

Populations in Faatoai Valley showed considerable variation in percentage of adults. Station 893, from 150–300 ft. elevation, had 20 of 65 (30.8%) adults; from Station 896 at 300 ft. elevation, there were only 19 of 182 (10.4%) adults. Station 900, also at 300 ft. elevation, had 11 of 73 (15.1%) adults. I doubt that sampling bias is involved, but there are insufficient data concerning the stations to suggest what factors might be responsible.

*Description of soft parts.*—Foot and tail slightly shorter than shell diameter. Sole undivided, pedal grooves prominent, uniting across tail, no caudal horn, middorsal groove weak. Head projecting in front of foot. Gonopore located slightly above and behind right rhinophore. Body color yellow-horn, usually with gray suffusion on head and neck.

Mantle collar (MC) with tapered edge, no glandular extension onto mantle roof. Pneumostome shielded by a weak right mantle lobe. Anus (A) and external ureteric pore (KX) in typical position just inside pneumostome.

Pallial region (fig. 39a) extending about  $\frac{1}{2}$  whorl apically. Lung roof without granulations. Kidney (K) bilobed, rectal lobe distinctly longer than pericardial, base tapering and extending apicad under intestinal loop, upper end medially indented. Length of kidney from anterior end of rectal lobe to base about 1.51 mm. Ureter (KD) following edges of kidney arms, a strip of lung roof visible between arms, opening next to anus. Heart (H) about half length of pericardial kidney arm. Principal pulmonary vein (HV) angling toward pneumostome, not conspicuously branched. Hindgut (HG) starting just above kidney apex, not tapering.

Ovotestis (fig. 39b) a clump of several finger-like lobes lying above stomach apex parallel to whorl sides, imbedded in digestive gland. Hermaphroditic duct (GD) as in *S. peasei*. Albumen gland (GG) and talon (GT) typical. Prostate (DG) with very few and large acini opening into tube lying inside uterine wall. Uterus (UT) bipartite, upper chamber thinner walled and narrower, lower with thick glandular walls.

Vas deferens (VD) much thicker apically, tapering to slender tube that remains constant in size until entering epiphallus. Epiphallus (E) without unusual features. Penial retractor (PR) arising from diaphragm near apex of pallial cavity, inserting as a U-shaped fan partly around epiphallus-penis junction. Penis (P) externally and internally the same as *S. peasei*, length about 1.00–1.10 mm. Atrium (Y) slender, rather short.

Free oviduct (UV), spermatheca (S), and vagina (V) without unusual structures.

(Based on BPBM 150416, 4 individuals, largest 3.49 mm. in diameter with  $4\frac{1}{4}$  whorls.)

### *Sinployea tahitiensis*, new species. Figures 38d–f, 39c–e.

*Diagnosis.*—Shell large, diameter 2.98–4.04 mm. (mean 3.50 mm.), with  $4\frac{1}{4}$  normally coiled whorls. Apex and early spire slightly and evenly elevated, body whorl descending more rapidly, spire protrusion about  $\frac{1}{6}$  of body whorl width, H/D ratio 0.428–0.541 (mean 0.498). Apical sculpture of 6–11 (mean 8.92) spiral cords. Postnuclear whorls with comparatively few, narrow, widely spaced, protractively sinuated radial ribs, 44–71 (mean 60.7) on the body whorl, whose interstices are 3–5 times their width. Ribs/mm. 4.67–8.37 (mean 5.86). Microsculpture of fine radial riblets, 8–12 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets with widely spaced secondary spiral cords whose interstices are about twice those of microradials. Umbilicus broadly open, V-shaped, last whorl decoiling rapidly, contained 3.38–4.50 times (mean 3.68) in the diameter, with rounded margins. Sutures channeled, whorls strongly rounded above, not compressed on basal margin.

The slightly elevated spire, more widely spaced secondary spiral cording, fewer apical cords and slightly narrower umbilicus combine to separate *Sinployea tahitiensis* (fig. 38d–f) from the relatively similar *S. lamellicosta* (fig. 40a–c). Both *S. modicella* (fig. 38a–c) and *S. neglecta* (fig. 41d–f) have many more radial ribs, whereas *S. montana* (fig. 41a–c) is much smaller and has a very narrow umbilicus.

*Description.*—Shell large, with  $4\frac{1}{4}$  loosely coiled whorls. Apex and first whorl and one-half flat, last whorl descending moderately, H/D ratio 0.478. Embryonic whorls 1%, with 10 relatively prominent spiral cords. Remaining whorls with protractively sinuated radial ribs having high periostracal lamellar extensions, 61 on the body whorl, whose interstices are 3–5 times their width. Microsculpture of fine radial riblets, 8–12 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Secondary spiral cording equal in size to microradials, twice as widely spaced. Umbilicus broadly open, strongly decoiling on last whorl, V-shaped, contained 3.47 times in the diameter. Color nearly uniform light reddish yellow with darker periostracal coloring on ribs. Aperture ovate, slightly flattened laterally above periphery, basal margin evenly rounded,



TABLE XVII. — LOCAL VARIATION IN SOCIETY ISLAND *SINPLOYEA*, I.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>modicella</u>					
Sta. 919 BPBM 150710	7	-----	1.67±0.056 (1.42-1.89)	3.29±0.059 (3.11-3.51)	0.508±0.0166 (0.430-0.553)
Sta. 900 BPBM 150473	11	-----	1.66±0.044 (1.39-1.95)	3.28±0.044 (3.01-3.54)	0.505±0.0087 (0.456-0.551)
Sta. 893 BPBM 150375	20	-----	1.75±0.028 (1.56-2.02)	3.34±0.026 (3.15-3.61)	0.523±0.0069 (0.480-0.598)
Sta. 896 BPBM 150416	19	-----	1.73±0.037 (1.36-2.05)	3.40±0.035 (3.18-3.71)	0.508±0.0085 (0.406-0.562)
Sta. 927 BPBM 150872	3	-----	1.72±0.051 (1.62-1.79)	3.39±0.090 (3.21-3.51)	0.509±0.0214 (0.471-0.546)
<u>tahitiensis</u>					
Sta. 867 BPBM 145702-3	5	61.5±6.52 (55-68)	1.94±0.050 (1.78-2.07)	3.74±0.110 (3.42-4.01)	0.519±0.0065 (0.500-0.541)
Sta. 862 BPBM 145166	4	-----	1.56±0.082 (1.38-1.78)	3.28±0.069 (3.19-3.49)	0.475±0.0173 (0.428-0.509)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>modicella</u>				
Sta. 919	4 1/8+(4 1/8-4 1/4)	0.85±0.037 (0.72-0.97)	3.89±0.106 (3.54-4.28)	9.00±0.69 (7-12)
Sta. 900	4 1/4-(4-4 3/8)	0.94±0.018 (0.85-1.05)	3.47±0.054 (3.16-3.77)	9.00±0.54 (7-12)
Sta. 893	4 1/4+(4-4 1/2)	0.98±0.017 (0.86-1.15)	3.40±0.043 (3.06-3.78)	9.58±0.33 (8-13)
Sta. 896	4 1/4+(4-4 5/8)	1.02±0.021 (0.86-1.22)	3.33±0.057 (2.95-3.79)	9.17±0.33 (7-12)
Sta. 927	4 1/4-(4 1/8-4 1/4)	0.93±0.061 (0.86-1.05)	3.64±0.162 (3.32-3.85)	-----
<u>tahitiensis</u>				
Sta. 867	4 1/2(4 3/8-4 5/8)	1.04±0.489 (0.92-1.12)	3.61±0.061 (3.41-3.75)	9.50±0.58 (9-10)
Sta. 862	4 1/8+(4-4 3/8)	0.93±0.041 (0.82-1.02)	3.55±0.126 (3.38-3.92)	7.50±0.65 (6-9)

inclined about 25° from shell axis. Height of holotype 1.74 mm., diameter 3.66 mm.

*Holotype*.—Society Islands: Tahiti, Station 863, Mt. Aorai Trail at 4,700–5,500 ft. elevation. Collected by Yoshio Kondo and Donald Anderson on September 14, 1934. BPBM 142072.

*Range*.—Interior of Tahiti at 770–6,300 ft. elevation, Society Islands.

*Paratypes*.—Tahiti: Fautaua Valley (Station 20) at 250 m. elevation (1 specimen, BPBM 136343); right fork of Papenoo Valley (Station 951) at 1,400 ft. elevation (2 specimens, BPBM 144969–70); Aorai Trail (Station 863) between 2nd and 3rd camps in leaf axils of *ieie* (3 specimens, BPBM 145913); ravine on west side (Station 862) of ridge crest, Mt. Aorai at 4,600 ft. elevation (6 specimens, BPBM 145166–7); Aorai Trail (Stations 865, 867) at 4,700–6,300 ft. elevation (10 specimens, BPBM 145296–7, BPBM 145702–3).

*Remarks*.—The flat spire and more numerous apical cords of *S. lamellicosta* (fig. 40a–c) are the systematically important conchological characters separating that species from *S. tahitiensis* (fig. 38d–f). The former was taken by Garrett at relatively low elevations and by the Mangarevan Expedition in a valley to one side of the Mt. Aorai Trail. It probably is geographically isolated from populations of *Sinployea tahitiensis*. *Sinployea montana* also was collected in a valley to the west of the Mt. Aorai Trail, but at 1,000 ft. higher elevation than *S. lamellicosta*. The Moorean *S. modicella* (fig. 38a–c) differs primarily in having twice as many radial ribs on the body whorl and fewer micro-radial riblets.

The penis (2.2–2.4 mm. long) is much larger than in either *S. lamellicosta* (1.4–1.5 mm. long) or *S. montana* (1.4–1.65 mm. long). Internally it shows no differences from the typical pattern.

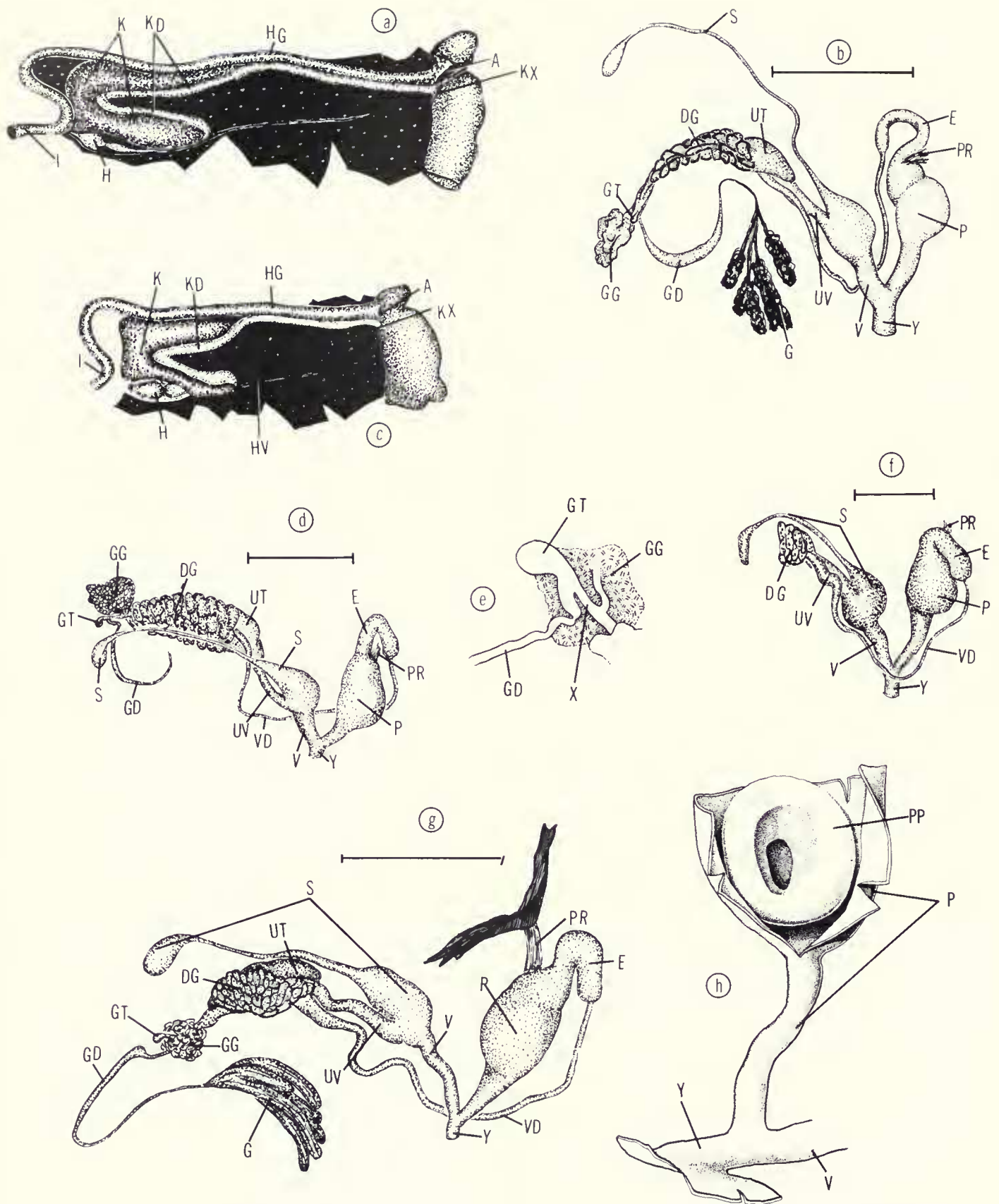


FIG. 39. Anatomy of Tahitian and Moorean *Sinployea*: **a-b**, *Sinployea modicello* (Férussac). Station 896, Faatoai, Moorea. BPBM 150416. **a**, pallial region. **b**, genitalia; **c-e**, *Sinployea tahitiensis*, new species. Station 867, Mt. Aorai, Tahiti. BPBM 145703. **c**, pallial region. **d**, genitalia. **e**, detail of talon-carrefour region; **f**, genitalia of *Sinployea montono*, new species. Station 866, Mt. Aorai, Tahiti. BPBM 145401; **g-h**, *Sinployea lomellicosto* (Garrett). Station 870, Mt. Aorai, Tahiti. BPBM 145537. **g**, genitalia. **h**, detail of stimulatory pad in penis. Scale lines equal 1 mm. (**a-d**, **f-g**, MO; **e**, **h**, MM).



Data on material from two local populations are presented in Table XVII. Specimens from Station 862 were subadult. This lower H/D ratio reflects the lessened body whorl descension as does the much lower mean height. The umbilical width is obviously less than in specimens of *S. lamellicosta* in the same size range. This provides a ready means of separating specimens where the spire protrusion is not obvious.

*Description of soft parts.*—Pallial region (fig. 39c) unusual only in having rectal and pericardial kidney arms equal in length, about 1.38 mm. long. Genitalia (fig. 39d) with head of talon less globular (fig. 39e) and a distinct shaft. Length of penis stalk, vagina, and atrium relatively short. Total length of penis about 2.2–2.4 mm. Interior of penis without unusual features. Jaw with plates partly fused. Radula typical, 6 laterals, with central slightly smaller.

(Based on BPBM 145703, 3 partial individuals.)

***Sinployea lamellicosta* (Garrett, 1884). Figures 39g–h, 40a–c.**

*Patula lamellicosta* Garrett, 1884, J. Acad. Nat. Sci., Philadelphia, 9 (1), p. 30, pl. 2, fig. 11 a, b—Tahiti, Society Islands.

*Helix (Patula) lamellicosta* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 39, pl. 8, figs. 33–34.

*Endodonta (Thaumatodon) lamellicosta* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 27.

*Endodonta (Charopa) lamellicostata (sic)* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35—typographical error.

*Diagnosis.*—Shell larger than average, diameter 2.78–3.55 mm. (mean 3.25 mm.), with 3¼–4¾ relatively loosely coiled whorls. Apex and spire flat or slightly depressed, body whorl descending sharply, H/D ratio 0.454–0.521 (mean 0.487), much lower than average. Apical sculpture of 10–16 (mean 12.5) rather fine spiral cords. Postnuclear sculpture of prominent, thin, protractively sinuated, widely spaced radial ribs, 43–71 (mean 52.4) on the body whorl, whose interstices are 4–6 times their width. Ribs/mm. 4.03–7.91 (mean 5.44). Microsculpture of fine radial riblets, 8–12 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets that can be seen on upper spire, plus secondary spiral cording whose spacing is equal to the microradials. Umbilicus broadly open, wide, cup-shaped, regularly decoiling, contained 2.89–3.87 times (mean 3.26) in the diameter, margins rounded. Whorl contours and apertural features normal.

*Sinployea lamellicosta* (fig. 40a–c) is the only Society Island species with a flat or slightly depressed spire. *Sinployea tahitiensis* (fig. 38d–f) is most similar, but has a slightly elevated spire, narrower umbilicus, and fewer spiral cords on the apex. All other Society Island species have much more crowded and numerous radial ribs. Extralimital species with flat or depressed spires all have much more numerous and crowded radial ribs.

*Description.*—Shell smaller than average, with slightly more than 3¾ loosely coiled whorls. Apex and early spire slightly depressed, body whorl descending rather rapidly, H/D ratio 0.440. Embryonic whorls 1¾, sculpture partially eroded, but remnants of 11 spiral ribs can be detected. Postnuclear whorls with protractively sinuated, prominent, widely spaced radial ribs, 50 on the body whorl, whose interstices are 4–6 times their width. Microsculpture of very fine radial riblets, 8–12 between each pair of major ribs, crossed by equal-sized secondary spiral cords that are slightly more widely spaced than the radial riblets, with barely visible, very fine and crowded spiral riblets most easily seen on upper spire. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above periphery, with evenly rounded basal margin. Color pale

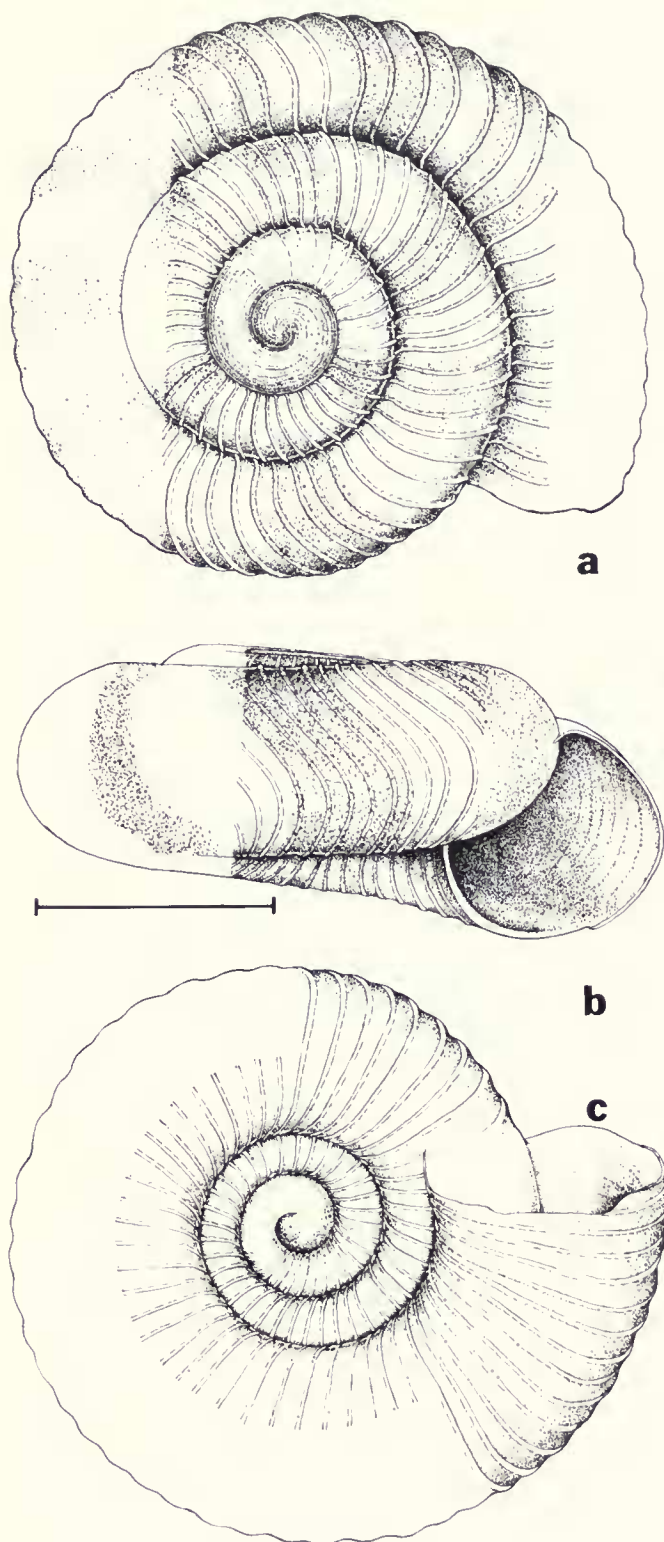


FIG. 40. a–c, *Sinployea lamellicosta* (Garrett). Tahiti, Society Islands. Lectotype. BPBM 2841. Scale line equals 1 mm. (MM).

yellow-horn with a few vague, light red flammulations. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.93 times in the diameter, margins rounded. Aperture ovate, strongly flattened laterally above periphery, with gently rounded basal margin, inclined about 15° from shell axis. Height of lectotype 1.19 mm., diameter 2.70 mm.

*Lectotype*.—Society Islands: Tahiti. Collected by Andrew Garrett. BPBM 2841.

*Range*.—Tahiti, Society Islands, at low (?) to high elevations, probably in only one or two valleys.

*Paratype*.—BPBM 2841.

*Material*.—Tahiti (6 specimens, BPBM 2841, Zurich, NMWC); Pirae-Aorai trail (1 specimen, BPBM 115855 Whitney Expedition); valley west of Aorai Trail (Station 870) at 5,000 ft. elevation (12 specimens, BPBM 145537-42).

*Remarks*.—Garrett (1884, p. 30) reported this to be "a scarce species, living beneath rotten wood in damp stations." Further collecting is needed to establish the exact geographic relationships of *S. lamellicosta*, *S. tahitiensis*, and *S. montana* in the Mt. Aorai region.

Whereas the lectotype is the smallest shell examined and is clearly subadult, the sculptural preservation was excellent, and it matches in form the Mangarevan Expedition material. A single juvenile collected by the Whitney South Sea Expedition (BPBM 115855) is tentatively referred here. The Zurich shells were barely adult and hence slightly higher and more narrowly umbilicated than the Mangarevan Expedition specimens. Only one-third of the latter were adult.

The flat spire and numerous apical cords are the main features characterizing *S. lamellicosta*.

*Description of soft parts*.—Pallial region with rectal and pericardial kidney arms almost equal in length, reaching 1.20 mm. long. No glandular extension onto pallial roof. Genitalia (fig. 39g) with rather long vagina. Penis quite thick, internal stimulatory pad (fig. 39h) very prominent. Length of penis about 1.4–1.5 mm. Glandular zone of spermatheca with a hardened sperm packet that was 0.45 mm. long, lower half cylindrical and 0.18 mm. in diameter, upper half expanded and spherical, diameter 0.28 mm. Radula typical, with 6 laterals.

(Based on BPBM 145537–8, 3 partly extracted specimens.)

### *Sinployea montana*, new species. Figures 39f, 41a–c.

*Diagnosis*.—Shell small, diameter 2.45–2.55 mm. (mean 2.50 mm.), with 3%–3% normally coiled whorls. Apex and spire moderately and evenly elevated, last portion of body whorl starting to descend more rapidly, spire protrusion between  $\frac{1}{4}$  and  $\frac{1}{5}$  body whorl width, with a high H/D ratio of 0.622–0.623 (mean 0.623). Apical sculpture of 13 spiral cords. Postnuclear sculpture of a few thin, prominent, protractively sinuated radial ribs, 57–69 (mean 63.0) on the body whorl, whose interstices are usually 3–4 times their width. Ribs/mm. 7.43–8.65 (mean 8.04). Microsculpture of fine radial riblets, 6–10 between each pair of major ribs, crossed by much finer and more crowded spiral riblets that become indistinct on body whorl. Umbilicus quite narrow, U-shaped, last whorl decoiling a little more rapidly, contained 5.93–8.55 times (mean 7.24) in the diameter, margins rounded. Basal margin of body whorl rounded, not flattened.

The high spire and very narrow umbilicus of *Sinployea montana* (fig. 41a–c) easily separate it from the other Society Island species. Its rib count is the same as in *S. tahitiensis* (fig. 38d–f), but the size difference produces a much more crowded ribbing in *S. montana*. All extralimital species of similar size have higher whorl counts, lower H/D ratios, and wider umbilici.

*Description*.—Shell small, with 3% loosely coiled whorls. Apex and early spire moderately and evenly elevated, last whorl descending sharply, H/D ratio 0.623. Embryonic whorls 1%, worn traces of about 13 relatively prominent spiral ribs remaining. Lower whorls with protractive, thin, radial ribs, 69 on the body whorl, whose interstices are 3–4 times their width. Microsculpture of fine radial riblets, 6–10 between each pair of major ribs, crossed by much finer and more crowded spiral riblets that become relatively indistinct on the body whorl. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above periphery, evenly rounded on lower palatal and basal margin. Umbilicus narrowly U-shaped, last whorl decoiling slightly more rapidly, contained 8.55 times in the diameter, margins rounded. Color uniform light yellow-horn with darker periostracal rib extensions, no flammulations. Aperture nearly circular, slightly flattened laterally above periphery and on basal margin, inclined about 10° from the shell axis. Height of holotype 1.58 mm., diameter 2.54 mm.

*Holotype*.—Society Islands: Tahiti, Station 866, valley west of Aorai Trail at 6,000 ft. elevation. Collected by Elwood Zimmerman, Yoshio Kondo, and Donald Anderson on September 15, 1934. BPBM 145401.

*Range*.—Mt. Aorai, 6,000 ft. elevation, Tahiti, Society Islands.

*Paratypes*.—Tahiti: valley west of Aorai Trail (Station 866) at 6,000 ft. elevation (2 specimens, BPBM 145401-2).

*Remarks*.—I suspect that the size of *Sinployea montana* is underrepresented by the available material. Two of the three examples showed only the first indications of gerontic growth. Probably 10%–15% greater diameter is attained.

No other Society or Cook species approaches *S. montana* in narrowness of the umbilicus. Only the Samoan *S. allecta* (fig. 54a–e) and the Fijian *S. recurva* (fig. 64c) could be confused on umbilical size. *Sinployea allecta* is 0.5 mm. larger and has an average of less than nine apical cords and a thicker body whorl. *Sinployea recurva* is still larger and has greatly reduced major sculpture.

*Description of soft parts*.—Pallial region typical, rectal arm longer than pericardial, former about 1.25 mm. long in one example. Apical genitalia not seen, lower portions typical. Penis 1.4–1.65 mm. long in two examples. Vergic papilla (fig. 39f) large and U-shaped, muscular bands relatively weak, stimulator typical.

Radula with 5–6 laterals and more than 6 marginals. Central 9  $\mu$  long, 7  $\mu$  wide, distinctly smaller than laterals, 1st lateral 8  $\mu$  wide.

(Based on BPBM 145401, 2 extracted and partly broken examples.)

### *Sinployea neglecta*, new species. Figures 41d–f, 42a.

*Diagnosis*.—Shell of average size, diameter 2.57–3.26 mm. (mean 2.83 mm.), with 3%–4% rather tightly coiled whorls. Apex and spire slightly to moderately and evenly elevated, body whorl descending more rapidly, spire protrusion  $\frac{1}{6}$ – $\frac{1}{5}$  of body whorl width, H/D ratio 0.441–0.632 (mean 0.536). Apical sculpture of 10–15 (mean 12.5) relatively fine spiral cords. Postnuclear sculpture of fine, prominent, thin, protractively sinuated radial ribs, 71–143 (mean 108.6) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 8.84–16.87 (mean 12.23). Microsculpture of fine radial riblets, 3–5 between each pair of major ribs, barely visible microspiral riblets and relatively prominent secondary spiral cords. Umbilicus of average width, V-shaped, last whorl usually decoiling



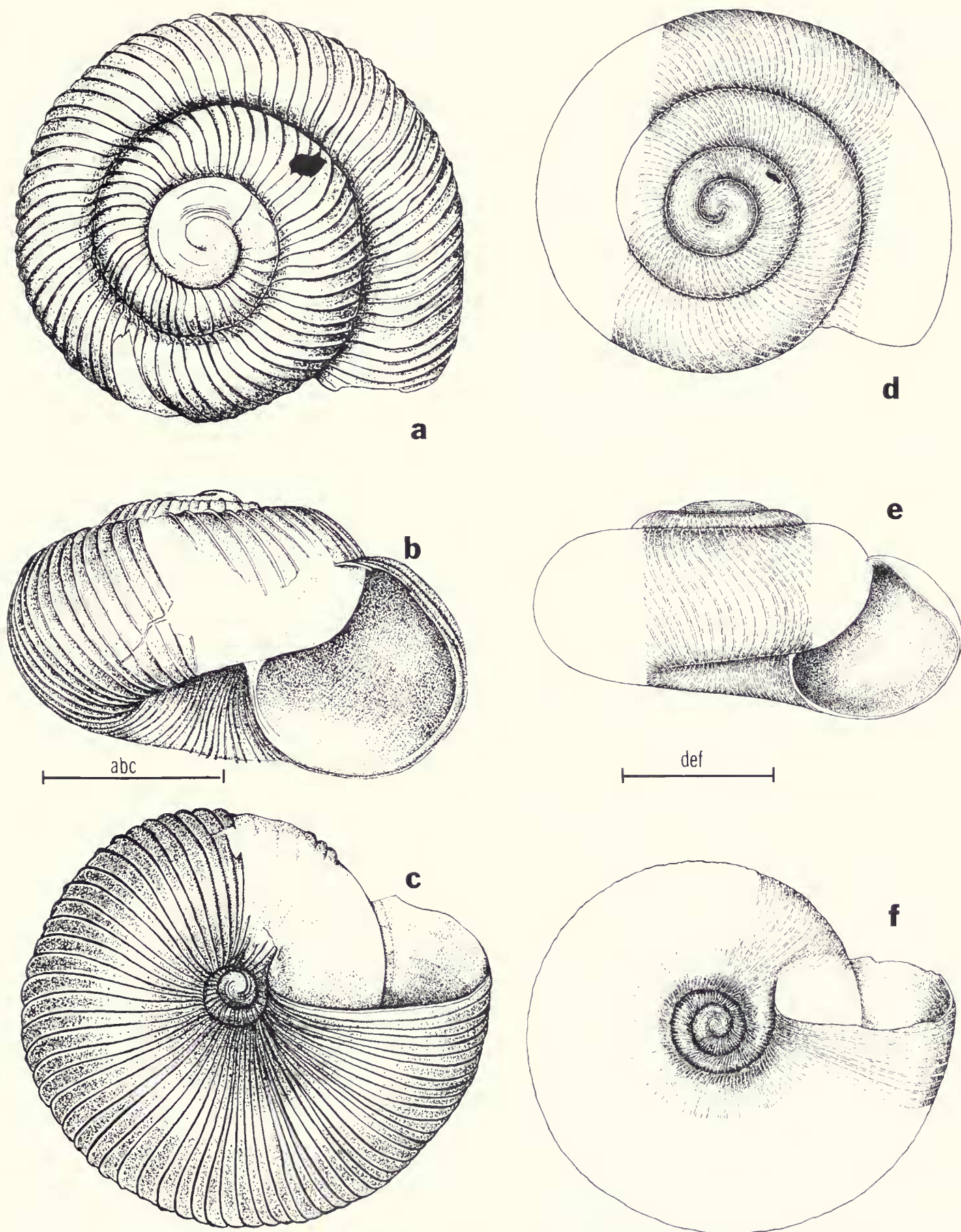


FIG. 41. **a-c**, *Sinployea montana*, new species. Station 866, Aorai Trail, 6,000 ft., Tahiti, Society Islands. Holotype. BPBM 145401; **d-f**, *Sinployea neglecta*, new species. Station 1008, Tiva, Huahine, Society Islands. Holotype. BPBM 151565. Scale lines equal 1 mm. (**a-c**, SG; **d-f**, MM).

slightly more rapidly, contained 3.21–5.00 times (mean 4.39) in the diameter, margins rounded. Whorl contours and apertural features without marked differences from average.

The smaller size, much narrower umbilicus, and greater number of apical cords separate *Sinployea neglecta* (fig. 41d–f) from the Moorean *S. modicella* (fig. 38a–c). *Sinployea* sp. from Borabora differs in the character of the ribbing, which is much lower and more rounded. Of the Cook Island species, *S. andrewi* (fig. 44a) has fewer apical cords and more radial ribs, whereas *S. atiensis* (fig. 44d–e) is more elevated and with slightly fewer apical cords. The Tongan *S. vicaria* (fig. 58a–d) has a U-shaped umbilicus, more rounded whorl contours, more microradial riblets, and more whorls.

**Description.**—Shell of average size, with 4 relatively loosely coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending slightly more rapidly, H/D ratio 0.530. Embryonic whorls  $1\frac{1}{2}$ , sculpture of about 12 spiral cords. Postnuclear whorls with numerous protractively sinuated, very thin radial ribs having periostracal lamellate extensions, 109 on the body whorl, whose interstices are variable, but about 2–3 times their width on middle of spire. Microsculpture of very fine radial riblets, 3–5 between each pair of major ribs, with almost equally large, slightly more widely spaced secondary spiral cords, and barely visible microspiral riblets. Sutures deeply impressed, whorls strongly rounded above, flattened laterally with rounded periphery and somewhat flattened basal margin. Color light reddish horn with indistinct darker reddish maculations visible mainly above periphery. Umbilicus relatively narrow, last whorl becoming more strongly decolled, contained 4.15 times in the diameter. Aperture ovate, flattened laterally above periphery and on basal margin, inclined about  $20^\circ$  from the shell axis. Height of holotype 1.45 mm., diameter 2.73 mm.

**Holotype.**—Society Islands: Huahine, Station 1008, 100 yd. inland, near Tiva at 6 ft. elevation. Collected on logs and dead leaves by Yoshio Kondo and Donald Anderson on October 3, 1934. BPBM 151565.

**Range.**—Huahine, Society Islands.

**Paratypes.**—Huahine (27 specimens, BPBM 6078, ANSP 1939, ANSP 47759, SMF 165460, ex SMF 165351); Tiva (Station 1008) about 100 yd. inland at 6 ft. elevation on logs and dead leaves (80 specimens, BPBM 151565–9); Fare (Stations 962, 963) at 100–300 ft. elevation under stones and logs or on dead leaves (52 specimens, BPBM 151121, BPBM 151144–9); Fare (Station 978) at 1,000–1,200 ft. elevation in a damp valley on dead fallen leaves (1 specimen, BPBM 151284). "Tahiti" (11 specimens, RSM).

**Remarks.**—Garrett (1884, p. 28) lumped this species with *S. modicella* (fig. 38a–c). *Sinployea neglecta* (fig. 41d–f) is much smaller, has more apical cords, a narrower umbilicus, and more prominent secondary spiral cording. These differences require better optical equipment and more precise measurements than could be made by Garrett. Several small samples from his collections and two larger sets from the Mangarevan Expedition are compared in Table XVIII. There are no significant size or shape differences, except in regard to umbilical width. The slightly wider umbilici for material from Station 1008 and ANSP 47759 is caused by a few gerontic individuals in which umbilical decoiling has proceeded further than usual,

producing relatively widely open umbilici and thus distorting the means.

Specimens from Tiva (Station 1008) were collected about 100 yd. inland in coastal vegetation, whereas those from Fare (Station 963) were found in lowland forest at 300 ft. elevation further inland. Percentage of adults was identical, with 15 of 51 (29.4%) from Station 963 and 24 of 81 (29.6%) from Station 1008. Size and shape differences reached significant levels, particularly in regard to height, with 37 degrees of freedom,  $t = 2.3293$ , and D/U ratio,  $t = 4.9127$ . Probably ecophenotypic variation is involved.

**Description of soft parts.**—Pallial region typical. Rectal kidney arm 1.45 mm. long, total cavity length 3.3 mm. Narrow strip of lung roof between ureter arms.

Genitalia (fig. 42a) without unusual features, penis length 1.4–1.6 mm. Drawing misleading in that slender shafts of penis and vagina folded under. Actual lengths as in *S. modicella*.

(Based on BPBM 151565, 4 partial examples.)

### *Sinployea* sp.

**Material.**—Society Islands: Borabora, south slope of Pahio-Temanu ridge (Station 1093) at 800 ft. elevation (1 specimen, BPBM 152395).

**Remarks.**—A single, probably subadult example from Borabora is not referable to any named form. The very low and crowded radial ribbing, 126 ribs on the body whorl, is more like some Western Polynesian species than any Society Island *Sinployea*. Measurements are given in Table XVI. Although obviously similar to *S. neglecta* in all dimensions, the character of the major ribbing is so distinctive that I doubt their identity. Both have three to six microradials between each pair of major ribs. Without more material and knowledge of the apical sculpture, description would be premature.

### COOK ISLAND *Sinployea*

Specimens of *Sinployea* have been found on all the major Cook Islands except Mauke. *Libera fratercula fratercula* (Pease) was collected on the latter island by P. H. Buck, who had taken *Sinployea* on Atiu, Aitutaki, and Mangaia during the same expedition. Hence, there is fair probability that this is an actual distributional gap.

*Sinployea atiensis* (Pease) lives on both Atiu and Aitutaki. Except for a slight increase in whorl count and a strongly elevated spire (fig. 44e), which increases the H/D ratio, this is a very average species in all measured characters (table XIX). *Sinployea andrewi* from Mangaia is slightly larger, has a greater number of more crowded major radial ribs (fig. 44a), is distinctly less elevated, has fewer microradials, and the umbilicus is V-shaped, rather than U-shaped. Rarotonga has, or had, a remarkable radiation of *Sinployea*, including nine of the 10 largest species in the genus. Only the Upolu Island *S. complementaria* (Mousson) (table XXIV) reaches larger size than the Rarotongan species.



TABLE XVIII. - LOCAL VARIATION IN SOCIETY ISLAND SINPLOYEA, II.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>lamellicosta</u>					
Sta. 870 BPBM 145537	4	50.0±4.05 (43-57)	1.69±0.030 (1.62-1.76)	3.49±0.046 (3.38-3.58)	0.485±0.0120 (0.454-0.510)
<u>montana</u>					
Sta. 866 BPBM 145401	2	-----	1.56±0.033 (1.52-1.59)	2.50±0.050 (2.45-2.55)	0.623±0.0005 (0.622-0.623)
<u>neglecta</u>					
Sta. 1008 BPBM 151565-7	24	-----	1.46±0.022 (1.29-1.62)	2.78±0.022 (2.58-2.98)	0.524±0.0067 (0.465-0.598)
Sta. 963 BPBM 151144,-7	15	-----	1.55±0.033 (1.39-1.82)	2.84±0.028 (2.72-3.08)	0.544±0.0096 (0.500-0.605)
ANSP 1939	3	107.3±5.36 (101-118)	1.52±0.033 (1.49-1.59)	2.84±0.098 (2.65-2.98)	0.538±0.013 (0.518-0.563)
ANSP 47759	5	107.5±12.66 (85-143)	1.55±0.065 (1.36-1.69)	2.91±0.070 (2.75-3.08)	0.541±0.028 (0.441-0.594)
BPBM 6078	6	-----	1.64±0.090 (1.39-1.99)	2.94±0.097 (2.65-3.28)	0.558±0.026 (0.455-0.632)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>lamellicosta</u>					
Sta. 870	4	1/4-(4 1/8-4 3/8)	1.14±0.037 (1.05-1.22)	3.06±0.0851 (2.89-3.29)	11.25±0.95 (10-14)
<u>montana</u>					
Sta. 866	3	5/8+(3 5/8-3 3/4)	0.36±0.066 (0.30-0.43)	7.24±1.31 (5.93-8.55)	-----
<u>neglecta</u>					
Sta. 1008	4	(3 5/8-4 3/8)	0.65±0.011 (0.59-0.82)	4.27±0.051 (3.60-4.72)	12.89±0.42 (10-15)
Sta. 963	4	+(3 7/8-4 1/4)	0.63±0.012 (0.56-0.72)	4.53±0.062 (4.00-4.94)	12.13±0.58 (10-15)
ANSP 1939	4	(3 3/4-4 1/8)	0.60±0.011 (0.59-0.63)	4.68±0.118 (4.45-4.84)	-----
ANSP 47759	4	1/8-(3 7/8-4 1/4)	0.72±0.062 (0.63-0.95)	4.04±0.222 (3.21-4.53)	-----
BPBM 6078	4	+(3 7/8-4 1/4)	0.64±0.053 (0.53-0.89)	4.64±0.233 (3.67-5.23)	-----

*Sinployea peasei* (fig. 45a-c) is the Rarotongan equivalent of *S. atiensis* and *S. andrewi*. Reduction of the apical sculpture (fig. 2a, p. 11) is the significant change, although (table XIX) there are minor size and shape differences from the other two species. *Sinployea peasei* is replaced in part of Avana Valley by *S. avanaensis* (fig. 45d-f). This is a much more narrowly umbilicated shell with many very crowded radial ribs and a lower whorl count. Present data are insufficient to determine whether there is a zone of sympatry. There does seem to be ecological separation, because only one of 159 *Sinployea peasei* collected in 1964 and 1965 was taken on the leaves of shrubs, the remainder under logs and stones. A few individuals of *S. avanaensis* were found under rotting wood, but the great majority were collected on tree trunks in moss and lichens from 1-15 ft. above ground level. Anatomical dif-

ferences between the two species are slight. *Sinployea avanaensis* has the rectal kidney lobe much wider, the penis about 0.3 mm. longer, and the vergic papilla longer and narrower than in *S. peasei*. Study of local populations in Avana Valley offers an excellent opportunity for investigation of speciation phenomena.

The larger species show two divergent patterns that may represent monophyletic series, plus two species, *S. planospira* (fig. 46d-h) and *S. rudis* (fig. 47d-f), that show individual specialization.

One series of species, *S. proxima*, *S. youngi*, *S. harveyensis*, and *S. canalis*, retains normal or slightly more crowded sculpture. The smallest, *S. proxima* (fig. 46a-c), has a distinctly channeled suture and relatively low spire. Garrett (1872, p. 230) reported it was a "common species lurking under stones and among rot-

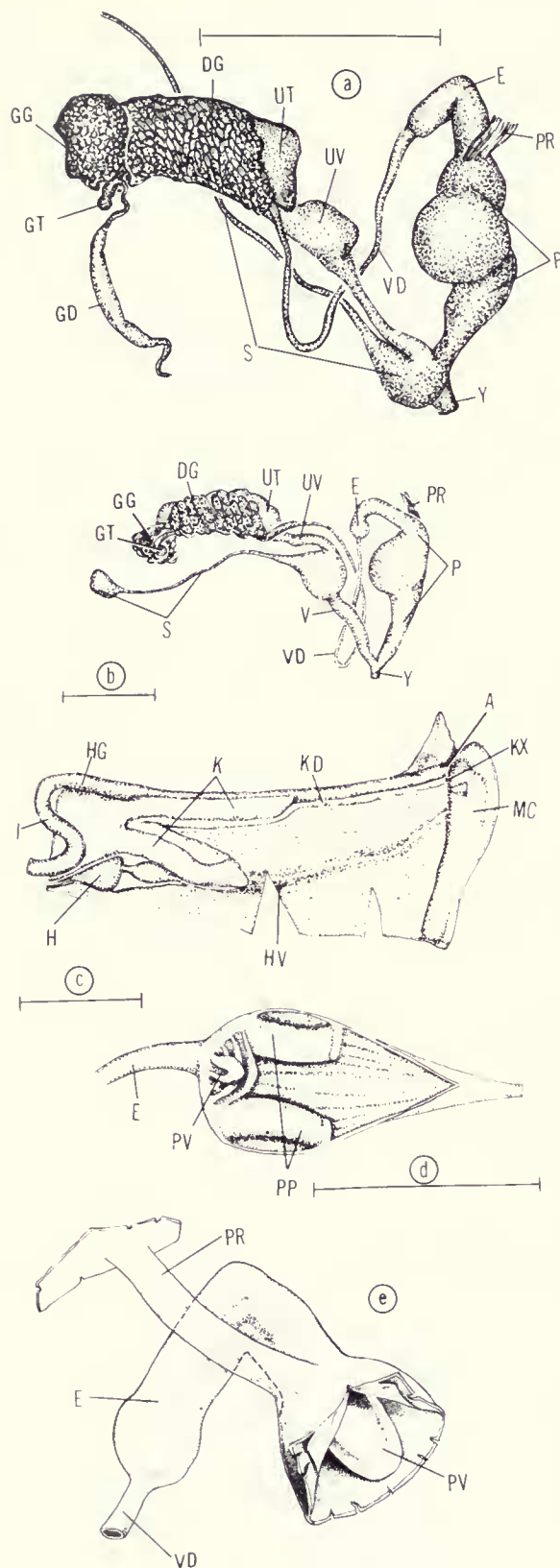


FIG. 42. Anatomy of Society and Cook Island *Sinployea*: a, genitalia of *Sinployea neglecta*, new species. Station 1008, Tiva, Huahine. BPBM 151565; b, genitalia of *Sinployea andrewi*, new species. Arakiore Oneroa, Mangaia, Cook Islands. BPBM 97652; c-e, *Sinployea peasei*, new species. Station 26, Mt. Maungaroa, 1,400 ft. elevation, Rarotonga, Cook Islands. FMNH 144645. c, pallial region. d, penial complex. e, detail of vergic papilla and muscular collar in penis. Scale lines equal 1 mm. (a-b, MO; e, MM; c-d, PS).

ten wood . . . in several villages (error for valleys)." Later Garrett (1881, p. 386) stated that it was "Not uncommon in several valleys." A personally annotated copy of Garrett (1872) corrected "villages" to "valleys." *Sinployea youngi* (fig. 48d-f) was taken "On the ground in damp woods, and only noticed in a single valley" (Garrett, 1872, p. 229). It is characterized by its large size, compressed aperture, and widely open umbilicus. *Sinployea harveyensis* (fig. 48a-c) is very similar to *S. youngi*, but has a higher spire, more numerous crowded ribs, narrower umbilicus, and ovate aperture. It was "A common species found under rotten wood" (Garrett, 1872, p. 228). *Sinployea canalis* (fig. 49a-c) was "found on the ground in damp forests, and confined to a single valley" (Garrett, 1872, p. 227). Although *S. planospira* (fig. 46d-h) retains typical sculpture, its great increase in whorl count (mean 6½), very wide umbilicus, flattened apex, plus early spire set it apart from the above species. *Sinployea planospira* is "a very rare species" (Garrett, 1881, p. 388). Its habitat was not defined.

The second series differs primarily in its much wider spacing of the major ribs. Quite probably it is polyphyletic. *Sinployea decorticata* (fig. 47a-c) has a higher spire and H/D ratio with between 10 and 20 microradials between each pair of major ribs and averages 75 ribs on the body whorl. It is confined to a single valley (Garrett, 1881, p. 387) where it was very abundant on the ground. *Sinployea otareae* (fig. 50a-c) has a lower spire and H/D ratio, averages about 96 ribs on the body whorl, and has only six to 10 microradial riblets between each pair of major ribs. It lived "under dead wood on the banks of a stream" in a valley about 3 miles away from that occupied by *S. decorticata*. *Sinployea tenuicostata* (fig. 50d-f) is much larger, has a flat apex, averages about 51 ribs on the body whorl, and has eight to 12 rather large microradial riblets between each pair of majors, indicating an increase in microradial riblet size and spacing. It was a "somewhat rare species, having a wide range on the island, and generally found on the ground on the sides of ravines." *Sinployea rudis* (fig. 47d-f) has reasonably typical upper spire sculpture, but the major ribs become sharply reduced and irregular on the body whorl, whereas the lateral flattening above the periphery has proceeded to form a broad and shallow suprapерipheral sulcus. It is thus an independent pattern of specialization. *Sinployea rudis* was a "very abundant species . . . we gathered hundreds in several valleys" (Garrett, 1881, p. 387). It was taken "on the ground in damp woods."

Of the large species, four (*S. proxima*, *S. harveyensis*, *S. tenuicostata*, and *S. rudis*) were widely distributed or found in several valleys, whereas five (*S. youngi*, *S. canalis*, *S. planospira*, *S. decorticata*, and *S. otareae*) were found only in a single valley. The niche of *S. planospira* was not defined, but all the other species were stated to occur on the ground or under rotting wood. Normally Garrett indicated sympatry for species. Thus, *Mautodontha zebrina* (Garrett) (see Solem, 1976b, p. 162) was collected in the same valley



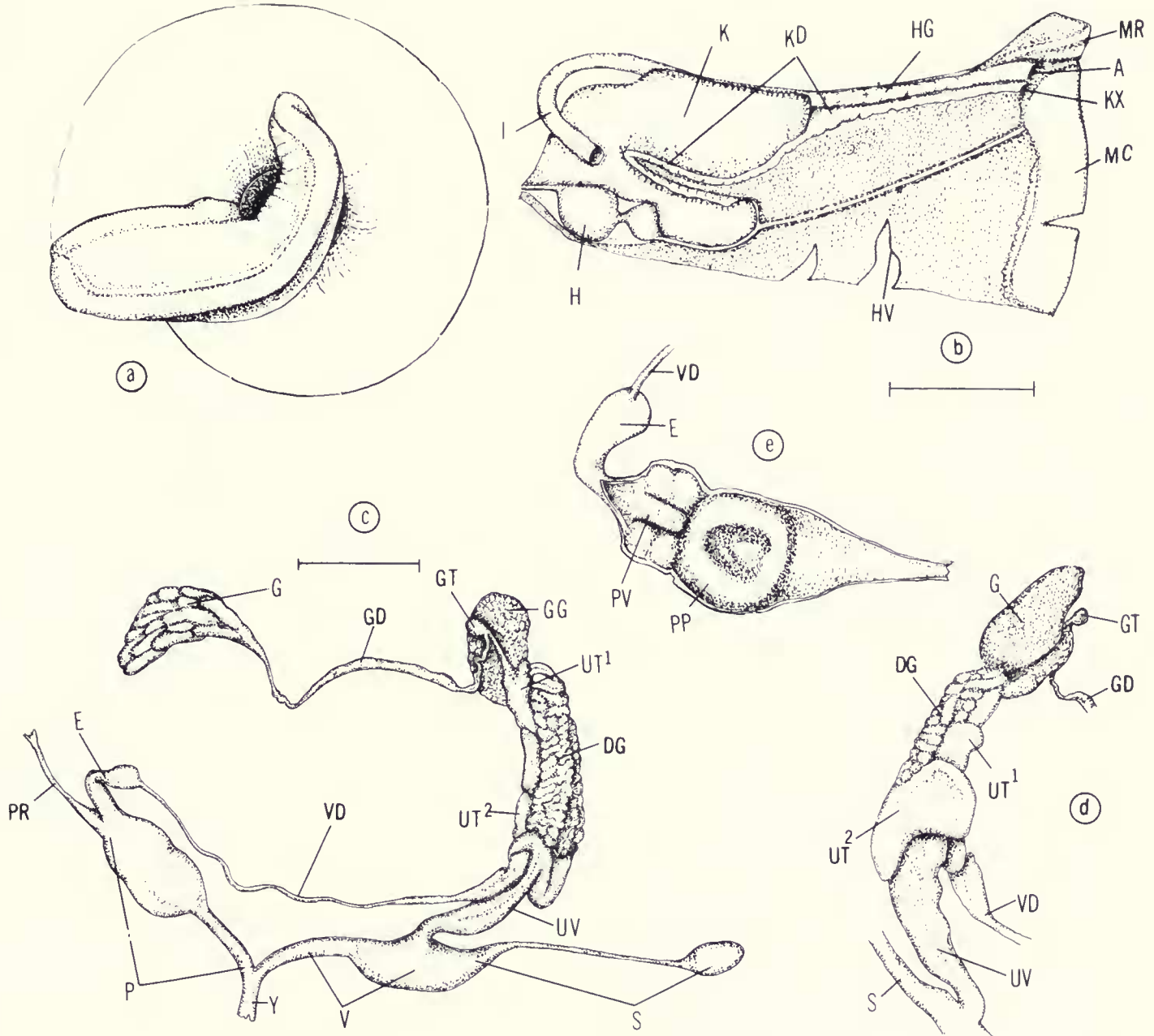


FIG. 43. Anatomy of *Sinployea avanaensis*, new species. Station 32A, Avana Valley, Rarotonga, Cook Islands. FMNH 144671: a, foot length in relation to shell diameter; b, pallial region; c, genitalia; d, midvisceral genitalia showing uterine sections; e, interior of penis. Scale lines equal 1 mm. (PS).

with *S. otareae*. *Sinployea youngi* was found in the same valley as *S. decorticata*, but Garrett did not state that they were sympatric. He made no other mention of any *Sinployea* being collected together. The probability is that these were geographically isolated.

Use of the past tense is deliberate. *Mautodontha unilamellata* (Garrett), *Thaumatodon multilamellatus* (Garrett), *Libera tumuloides* (Garrett), *Libera subcavernula* (Tryon), *Mautodontha zebrina* (Garrett), and the nine large *Sinployea* were not collected in 1964 or 1965 despite rather extensive coverage of different valleys. Overlooking the highly localized species, such as "one-half acre . . . nearly two miles inland" (*Libera tumuloides*), would not be difficult, but the total failure

to find any of the widely distributed species suggests that actual extinction has occurred. There has been no recent comprehensive report on the ant fauna of Rarotonga, but *Pheidole megacephala* (Fabricius), a species very destructive to native insects, has been on Rarotonga since at least 1914 (Wilson & Taylor, 1967b, p. 47). The same ant is common on Upolu where *Sinployea complementaria* (Mousson) still occurs, but that species is semiarbooreal (p. 129) and the shift in habitat from litter to semiarbooreal may have allowed coexistence of the ant and snail. Possibly some species still survive at higher elevation in isolated colonies, but I suspect that most of the Rarotongan endodontoids are extinct.

TABLE XIX. - RANGE OF VARIATION IN COOK ISLAND SINPLOYEA.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO			
<u>atiensis</u> (Pease)	39	93.3(83-107)	11.27(10.4-12.5)	1.57(1.29-1.92)	2.70(2.45-3.18)	0.582(0.527-0.642)			
<u>andrewi</u>	83	129.2(104-158)	14.01(11.63-16.09)	1.54(1.29-1.69)	2.95(2.68-3.15)	0.519(0.472-0.568)			
<u>peasei</u>	173	112.2(83-167)	11.51(8.80-14.66)	1.62(1.25-1.94)	3.15(2.97-4.01)	0.492(0.415-0.558)			
<u>avanaensis</u>	138	225.8(175-290)	20.82(16.28-25.1)	1.52(1.32-1.81)	3.21(2.86-3.82)	0.474(0.427-0.516)			
<u>proxima</u> (Garrett)	20	119.7(92-154)	10.75(8.91-12.96)	1.97(1.71-2.37)	3.61(3.26-4.08)	0.544(0.519-0.583)			
<u>planospira</u> (Garrett)	3	128.0(108-148)	10.62(10.05-11.19)	1.77(1.52-2.22)	3.74(3.44-4.24)	0.468(0.439-0.524)			
<u>rudis</u> (Garrett)	32	RIBS REDUCED		2.23(1.97-2.83)	4.04(3.68-4.83)	0.553(0.500-0.642)			
<u>decorticata</u> (Garrett)	21	75.0(62-103)	5.61(4.84-6.47)	2.36(2.04-2.98)	4.30(3.71-5.10)	0.550(0.488-0.590)			
<u>harveyensis</u> (Garrett)	27	RIBS REDUCED		2.39(1.92-3.01)	4.35(3.91-5.23)	0.550(0.475-0.641)			
<u>youngi</u> (Garrett)	17	115.4(96-139)	8.13(7.15-9.68)	2.27(1.84-2.66)	4.54(3.75-5.07)	0.499(0.457-0.553)			
<u>canalis</u> (Garrett)	18	119.8(98-146)	8.22(7.07-9.74)	2.14(1.84-2.63)	4.63(4.01-5.46)	0.463(0.427-0.544)			
<u>otareae</u> (Garrett)	38	95.6(81-116)	6.48(5.72-7.73)	2.41(2.07-2.96)	4.68(4.21-5.20)	0.516(0.470-0.570)			
<u>tenuicostata</u> (Garrett)	15	50.7(43-66)	3.46(2.87-4.23)	2.34(1.94-2.63)	4.70(4.08-5.43)	0.499(0.437-0.537)			
	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BW		
<u>atien.</u>	4 3/8-(4 1/8-4 7/8)	0.63(0.56-0.82)	4.26(3.77-4.82)	11.13(9-14)	0.21(0.16-0.26)	0.86(0.79-0.99)	0.237(0.196-0.296)		
<u>andre.</u>	4 1/8+(4-4 3/8)	0.72(0.63-0.79)	4.09(3.74-4.45)	9.19(8-11)	0.17(0.13-0.23)	0.91(0.86-0.95)	0.189(0.143-0.269)		
<u>pease.</u>	4 3/8-(4-5 1/8)	0.81(0.56-1.25)	3.93(3.72-4.60)	11.4(9-14)	0.18(0.10-0.30)	0.93(0.82-1.02)	0.176(0.103-0.300)		
<u>avana.</u>	4+(3 7/8-4 1/2)	0.69(0.53-0.99)	4.78(3.87-5.69)	10-14 VERY FINE	0.17(0.12-0.23)	0.95(0.79-1.09)	0.181(0.113-0.264)		
<u>proxi.</u>	4 3/8-(4-4 7/8)	0.68(0.59-0.76)	5.35(4.48-6.16)		0.15(0.10-0.23)	1.17(1.05-1.32)	0.124(0.091-0.175)		
<u>plano.</u>	6 5/8(6 1/4-7 1/4)	1.28(1.15-1.41)	2.90(2.75-2.98)		0.23	1.02	0.226		
<u>rudis</u>	4 1/4+(3 7/8-4 5/8)	0.83(0.69-1.12)	4.87(4.18-5.62)	10.02(8-12)	0.24(0.20-0.43)	1.32(1.18-1.45)	0.184(0.150-0.296)		
<u>decor.</u>	4 5/8-(4 3/8-5)	1.00(0.79-1.22)	4.32(3.75-5.92)	9.00(8-10)	0.27(0.13-0.46)	1.29(1.18-1.58)	0.209(0.103-0.292)		
<u>harve.</u>	4 5/8+(4 1/4-5)	0.92(0.76-1.18)	4.73(3.65-5.48)		0.36(0.20-0.59)	1.39(1.28-1.55)	0.258(0.150-0.450)		
<u>young.</u>	4 3/8+(3 7/8-5)	1.23(1.03-1.61)	3.73(3.15-4.39)	10.73(10-12)	0.21(0.15-0.30)	1.39(1.22-1.51)	0.149(0.116-0.196)		
<u>canal.</u>	5-(4 1/2-5 1/2)	1.59(1.38-1.84)	2.91(2.64-3.10)	10.21(8-12)	0.15(0.10-0.26)	1.53(1.41-1.74)	0.096(0.067-0.151)		
<u>otare.</u>	4 3/4(4 1/2-5)	1.15(0.89-1.41)	4.10(3.47-5.52)	9.41(8-12)	0.25(0.13-0.40)	1.45(1.35-1.55)	0.171(0.093-0.261)		
<u>tenui.</u>	4 1/4(3 7/8-4 1/2)	0.92(0.79-1.18)	5.16(4.29-6.20)	10.45(9-12)	FLAT	1.56(1.44-1.64)	FLAT		

KEY TO THE RAROTONGAN *Sinployea*

- Whorls less than 5 1/8 ..... 2  
Whorls more than 6 1/8 ..... *Sinployea planospira* (Garrett, 1881)
- Radial ribs crowded to widely spaced ..... 4  
Radial ribs too crowded to count on body whorl only ..... 3
- Body whorl with supraperipheral sulcus; ribs reduced to irregularity ..... *Sinployea rudis* (Garrett, 1872)  
Body whorl without sulcus; ribs very crowded ..... *Sinployea harveyensis* (Garrett, 1872)
- Suture normal ..... 5  
Suture distinctly channeled (fig. 46a-b) ..... *Sinployea proxima* Garrett, 1872
- Mean diameter less than 3.5 mm ..... 6  
Mean diameter more than 4.0 mm ..... 7
- Mean rib count over 200; mid-Avana Valley ..... *Sinployea avanaensis*, new species  
Mean rib count less than 140; widely distributed ..... *Sinployea peasei*, new species
- Mean ribs/mm. about 8 ..... 8  
Mean ribs/mm. 3-7 ..... 9
- Umbilicus widely open, mean D/U ratio about 3.00; whorls strongly compressed laterally ..... *Sinployea canalis* (Garrett, 1872)  
Umbilicus of normal width, mean D/U ratio about 3.75; whorls compressed laterally above periphery ..... *Sinployea youngi* (Garrett, 1872)
- Spire flat, mean rib count about 50 ..... *Sinployea tenuicostata* (Garrett, 1872)  
Spire strongly elevated; mean rib count 75-100 ..... 10



10. Mean rib count about 75; 10–20 microradials between each pair of major ribs.....*Sinployea decorticata* (Garrett, 1872)  
Mean rib count about 95; 6–10 microradials.....  
*Sinployea otareae* (Garrett, 1872)

***Sinployea atiensis* (Pease, 1870). Figure 44d–f.**

*Pithys atiensis* Pease, 1870, J. de Conchyl., 18, pp. 394–395—Atiu, Cook Islands.

*Pitys atiensis* Pease, 1871, Proc. Zool. Soc. London, 1871, pp. 453, 474.

*Helix atiensis* (Pease), Pfeiffer, 1876, Monog. helic. viv., 7, p. 165.

*Patula atiensis* (Pease), Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 386—Atiu and Aitutaki, Cook Islands.

*Endodonta* (*Charopa*) *modicella* var. *atiensis* (Pease), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

**Diagnosis.**—Shell slightly smaller than average, diameter 2.45–3.18 mm. (mean 2.70 mm.), with 4¼–4¾ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, last whorl descending more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.527–0.642 (mean 0.582). Apical sculpture of 9–14 (mean 11.13) prominent spiral cords. Postnuclear whorls with narrow, prominent, crowded, protractively sinuated radial ribs, 83–107 (mean 93.3) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 10.4–12.5 (mean 11.27). Microsculpture of fine radial riblets, 5–8 between each pair of major ribs, crossed by very fine and crowded spiral riblets, with a secondary sculpture of rather widely spaced spiral cords. Umbilicus rather narrow, U-shaped, regularly decoiling, contained 3.77–4.82 (mean 4.26) in the diameter, margins rounded. Whorl and apertural characters not differing from average pattern.

*Sinployea atiensis* (fig. 44d–f) has lower and more rounded radial ribs than any of the Society Island species. Its high spire, slightly greater whorl count, and finer apical cords separate it from *S. neglecta* (fig. 41d–f). The related *S. andrewi* (fig. 44a–c) and *S. peasei* (fig. 45a–c) are distinctly less elevated and larger; *S. andrewi* has fewer and finer apical cords; *S. peasei* has the apical cords greatly reduced in prominence.

**Types.**—No specimens dating from Pease's exchanges could be located. The possibility of specimens being discovered in some European museum is good, and I prefer not to designate a neotype.

**Range.**—Atiu and Aitutaki, Cook Islands.

**Material.**—Aitutaki (5 specimens, Zurich): Reureu, ½ mile inland at 100 ft. elevation (1 specimen, BPBM 95649). Atiu (13 specimens, BPBM 87407–9, Zurich): Matai, ¼ mile inland at 50 ft. elevation (11 specimens, BPBM 95117); below Tengtangi, 1½ miles inland at 150 ft. elevation (1 specimen, BPBM 94942); Lake Teroto, ½ mile inland at 50 ft. elevation (4 specimens, BPBM 95036); Mokoero, ½ mile inland at 30 ft. elevation (2 specimens, BPBM 95141); Tarapaku track, ¼ to ½ mile inland at 50 ft. elevation (2 specimens, BPBM 94998).

**Remarks.**—Although Garrett (1884, p. 28) considered this to be a synonym of the Moorean *S. modicella* (fig. 38a–c), the qualitative difference in ribbing and obvious changes in proportions (tables XVI, XIX) effectively separate the two species. As with the Ancey collection, Pease's types and exchanges were so widely scattered that I prefer not to select a type specimen at this time. The Aitutaki examples were barely adult, and hence I attach no systematic significance to the

smaller size and lower spire shown by this set (table XX).

**Description of soft parts.**—Partial dissection of several fragmentary examples showed no differences in structures from *S. peasei*. Penis about 1.1–1.3 mm. long, most examples flattened too badly for opening. One specimen with verge and stimulatory pad identical to *S. peasei*.

(Based on BPBM 95117, several examples.)

***Sinployea andrewi*, new species. Figures 42b, 44a–c.**

**Diagnosis.**—Shell slightly larger than average, diameter 2.68–3.15 mm. (mean 2.95 mm.), with 4–4¾ normally coiled whorls. Apex and spire slightly to moderately and evenly elevated, body whorl descending more rapidly, spire protrusion less than ½ body whorl width, H/D ratio 0.472–0.568 (mean 0.519). Apical sculpture of 8–11 (mean 9.19) prominent spiral cords. Postnuclear sculpture of narrow, rounded, crowded, protractively sinuated radial ribs, 104–158 (mean 129.2) on the body whorl, whose interstices usually are less than twice their width. Ribs/mm. 11.63–16.09 (mean 14.01). Microsculpture of fine radial riblets, 3–6 between each pair of major ribs, with barely visible microspirals and rather crowded secondary spiral cording. Umbilicus open, V-shaped, last whorl decoiling more rapidly, contained 3.72–4.60 times (mean 4.09) in the diameter, margins rounded. Whorl contour and apertural features normal.

*Sinployea andrewi* (fig. 44a–c) has a lower spire, more numerous and crowded radial ribs, and fewer apical cords than *S. atiensis* (fig. 44d–f). *Sinployea peasei* (fig. 45a–c) is larger, with the apical cording reduced in prominence. Society Island species have much finer and higher radial ribs. *Sinployea rotumana* (Smith) (Fig. 61d–f) has fewer, slightly more widely spaced and distinctly narrower radial ribs, a U-shaped umbilicus, and more crowded secondary spiral cording.

**Description.**—Shell of average size, with 4¼ moderately loosely coiled whorls. Apex and spire moderately and almost evenly elevated, last whorl descending more rapidly, H/D ratio 0.516. Apical whorls slightly more than 1¾, partly worn, sculpture of 10 spiral ribs. Postnuclear whorls with closely set, rounded, protractively sinuated radial ribs, 158 on the body whorl, whose interstices are less than twice their width. Microsculpture of 3–6 fine radial riblets between each pair of major ribs, closely set and equally prominent secondary spiral cords, and barely visible spiral riblets. Sutures moderately impressed, whorls shouldered above, flattened laterally above rounded periphery, with slightly flattened basal margin. Color dark reddish yellow, with occasional lighter streaks. Umbilicus moderately open, V-shaped, last whorl decoiling more sharply, contained 4.13 times in the diameter. Aperture subcircular, strongly flattened laterally above periphery, slightly flattened basally, inclined about 30° from shell axis. Height of holotype 1.61 mm., diameter 3.12 mm.

**Holotype.**—Cook Islands: Mangaia, Arakiore Oneroa, ¾ mile from shore at 125 ft. elevation. Collected by P. H. and M. Buck on February 16, 1930. BPBM 97652.

**Range.**—Mangaia, Cook Islands.

**Paratypes.**—Mangaia: Arakiore Oneroa, ¾ mile from shore at 125 ft. elevation (82 specimens, BPBM 97652–3); Oneroa, ½ mile inland under stones at 115 ft. elevation (1 specimen, BPBM 97544).

**Remarks.**—The appearance of *Sinployea andrewi* (fig. 44a–c) is very similar to that of *S. neglecta* (fig. 41d–f) from Huahine, Society Islands, and it is difficult to find shell characters that immediately separate individuals of the two species. In general, *S. andrewi* has less sharply impressed sutures and wider, more crowded radial ribs with a lesser average number of

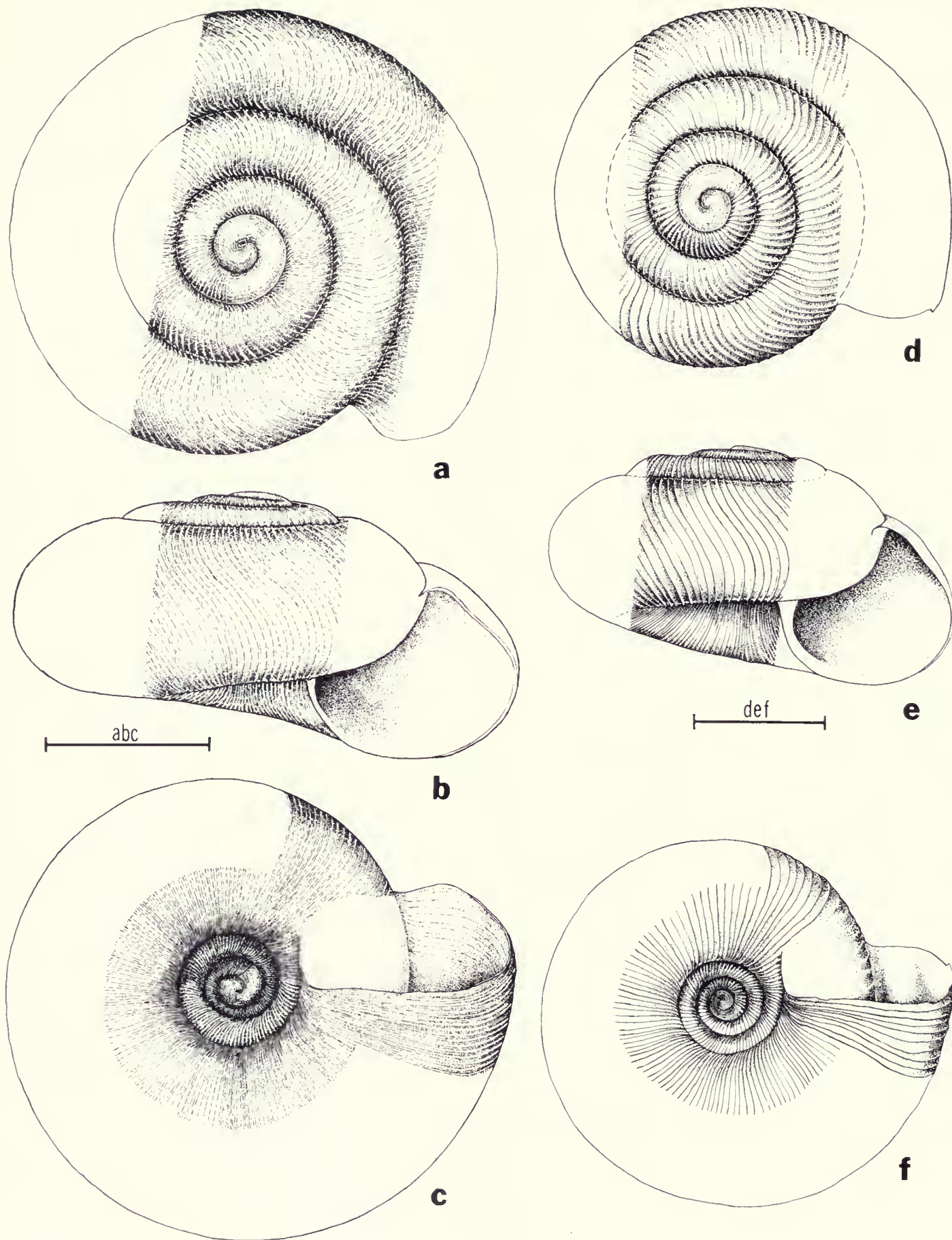


FIG. 44. a-c, *Sinployea andrewi*, new species. Arakiore, Mangaia, Cook Islands. Holotype. BPBM 97652; d-f, *Sinployea atiensis* (Pease). Matai, Atiu, Cook Islands. BPBM 95117. Scale lines equal 1 mm. (a-c, MM; d-f, SH).



TABLE XX. - LOCAL VARIATION IN COOK ISLAND SINPLOYEA, I.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>atiensis</u>					
Aitutaki Zurich	3	85.3±1.45 (83-88)	1.36±0.038 (1.29-1.42)	2.51±0.039 (2.45-2.58)	0.540±0.0069 (0.527-0.551)
Atiu BPBM 95117	9	-----	1.57±0.034 (1.46-1.79)	2.71±0.063 (2.55-3.18)	0.581±0.0083 (0.543-0.616)
Zurich	5	94.4±2.64 (86-102)	1.55±0.024 (1.49-1.62)	2.65±0.058 (2.50-2.83)	0.584±0.0067 (0.573-0.609)
BPBM 87407, 94942,-98, 95036,-141	8	-----	1.64±0.059 (1.39-1.92)	2.75±0.063 (2.55-3.01)	0.596±0.013 (0.539-0.642)
<u>andrewi</u>					
BPBM 96652-3	24	-----	1.54±0.018 (1.29-1.69)	2.95±0.022 (2.68-3.15)	0.519±0.0043 (0.472-0.568)
<u>avanaensis</u>					
Sta. 18a <sup>2</sup> FMNH 144631-2	16	233.3 (175-290)	1.54±0.031 (1.32-1.81)	3.21±0.060 (2.86-3.68)	0.479±0.0062 (0.438-0.516)
Sta. 32a FMNH 144671	6	-----	1.47±0.062 (1.32-1.74)	3.22±0.150 (2.89-3.82)	0.459±0.0086 (0.427-0.489)
<u>proxima</u>					
Zurich, AMS	5	110.0±6.60 (92-129)	1.85±0.056 (1.72-2.05)	3.50±0.068 (3.31-3.68)	0.529±0.0076 (0.518-0.559)
ANSP 47700	5	130.2±8.72 (104-154)	1.96±0.087 (1.79-2.22)	3.55±0.109 (3.28-3.81)	0.551±0.0088 (0.534-0.583)
BPBM 2317	5	129 (116-142)	2.09±0.087 (1.89-2.38)	3.79±0.088 (3.61-4.11)	0.551±0.0103 (0.523-0.580)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>atiensis</u>					
Aitutaki Zurich	4 1/4-(4 1/8-4 1/4)	0.59±0.010 (0.58-0.61)	4.21±0.012 (4.19-4.23)	10.67±0.335 (10-11)	
Atiu BPBM	4 1/4+(4 1/8-4 5/8)	0.64±0.025 (0.56-0.82)	4.16±0.090 (3.77-4.59)	11.86±0.669 (9-14)	
Zurich	4 1/4+(4 1/8-4 1/2)	0.61±0.017 (0.56-0.66)	4.36±0.148 (3.87-4.70)	-----	
BPBM	4 1/2-(4 1/4-4 7/8)	0.65±0.019 (0.59-0.72)	4.35±0.088 (4.05-4.82)	10.5±0.646 (9-12)	
<u>andrewi</u>					
BPBM	4 1/8+(4-4 3/8)	0.72±0.010 (0.63-0.79)	4.09±0.041 (3.74-4.45)	9.19±0.203 (8-11)	
<u>avanaensis</u>					
Sta. 18a	4+(3 3/4-4 3/8)	0.67±0.025 (0.53-0.86)	4.88±0.121 (4.24-5.76)	-----	
Sta. 32a	4 1/8+(4-4 1/2)	0.75±0.057 (0.63-0.99)	4.50±0.168 (3.87-4.96)	-----	
<u>proxima</u>					
Zurich	4 1/4-(4-4 3/8)	0.65±0.022 (0.59-0.72)	5.35±0.107 (5.00-5.55)	-----	
ANSP	4 1/4+(4-4 5/8)	0.69±0.029 (0.59-0.76)	5.16±0.246 (4.48-5.75)	-----	
BPBM	4 1/2-(4 1/4-4 7/8)	0.68±0.028 (0.59-0.76)	5.53±0.206 (4.96-6.16)	-----	

apical ribs. The differences are sufficient that I can readily separate individuals on the basis of sculpture, but I cannot satisfactorily quantify the change.

This species is named after Andrew Garrett, pioneer collector and student of Cook Island land shells.

*Description of soft parts.*—Dissection of several individuals showed no differences from *S. peasei*. Penis length was about 1.1–1.3 mm., with internal sculpture typical. Partial figuring (fig. 42b) of the genitalia is provided.

Radula without unusual features.

(Based on BPBM 97652, 6 individuals).

***Sinployea peasei*, new species.** Figures 2a–b, 42c–e, 45a–c.

*Patula atiensis* (Pease), Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 386—Rarotonga, Cook Islands (partly).

*Diagnosis.*—Shell rather large, diameter 2.97–4.01 mm. (mean 3.15 mm.), with 4–5% normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, spire protrusion a little more than  $\frac{1}{6}$  body whorl width, H/D ratio 0.415–0.558 (mean 0.492). Apical sculpture of 9–14 (mean 11.4) very faint spiral cords (fig. 2a–b) that cannot be counted on most examples. Postnuclear whorls with prominent, protractively sinuated, rounded radial ribs, 83–167 (mean 112.2) on the body whorl, whose interstices are usually 2–3 times their width. Ribs/mm. 8.80–14.66 (mean 11.51). Microsculpture of fine radial riblets, 4–8 between each pair of major ribs, extremely fine spiral riblets, and irregular secondary spiral cording. Umbilicus open, V-shaped, last whorl deciling more rapidly, contained 3.72–4.60 times (mean 3.93) in the diameter, margins rounded. Whorl contours (fig. 2a) and apertural shape typical.

*Sinployea peasei* has the apical cording (fig. 2a) greatly reduced in prominence, but differs only slightly in size and proportions from the other small Cook Island species. *Sinployea modicella* (Férussac) from Moorea is more widely umbilicated, has finer major radial ribbing, and fewer, much more prominent apical cords (fig. 1b).

*Description.*—Shell large, with 4% normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.495. Apical whorls 1%, sculpture of about 12 spiral cords, partly worn over most of surface. Postnuclear whorls with prominent, protractively sinuated, lamellate radial ribs, 113 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of very fine radial riblets, 4–8 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets, with weak secondary spiral cording that becomes conspicuous only in the umbilicus. Sutures deep, whorls strongly rounded above, markedly flattened laterally above periphery with slightly compressed basal margin, umbilical margin evenly rounded. Color yellow-horn, with broad and somewhat irregular reddish flammulations that do not fade out on shell base. Umbilicus broadly open, V-shaped, last whorl deciling more rapidly, contained 3.62 times in the diameter. Aperture ovate, strongly flattened laterally above periphery, inclined about 30° from shell axis. Height of holotype 1.71 mm., diameter 3.45 mm.

*Holotype.*—Cook Islands: Rarotonga, Station 26, west slopes of Mt. Maungaroa at 1,400 ft. elevation. Collected under dead wood by Laurie Price in December, 1964. FMNH 155947.

*Range.*—Widely spread over inland areas of Rarotonga, Cook Islands.

*Paratypes.*—Rarotonga (9 specimens, BPBM 2331, BPBM 8585): lower slopes of Mt. Maungaroa at 600 ft.

elevation (1 specimen, BPBM 79780); Takuvaine Valley (Station 2) at 200 ft. elevation (1 specimen, FMNH 144519); above Takuvaine stream (Station 4) at 400 ft. elevation (9 specimens, FMNH 144547); upper Takuvaine Valley (Station 5a), near Mt. Te Kou at 1,000 ft. elevation (1 specimen, FMNH 144553); Mt. Te Manga, Takuvaine Valley (Station 30) at 1,200 ft. elevation (12 specimens, FMNH 144644); north slope (Station 3) of Mt. Maungaroa at 1,000 ft. elevation (9 specimens, FMNH 144536); Mt. Ikurangi (Station 8) at 800 ft. elevation (11 specimens, FMNH 144567–8); Taipara Valley (Station 10) at 400 ft. elevation (8 specimens, FMNH 144578); west slope of Mt. Maungaroa (Station 26) at 1,400 ft. elevation (33 specimens, FMNH 144645–6); Avana Valley (Station 14) at 300 ft. elevation (32 specimens, FMNH 144613–4); Avatiu Valley (Stations 11, 28) at 500–600 ft. elevation (14 specimens, FMNH 144586, FMNH 144652); south slope of Mt. Te Rua Manga (Station 29) at 1,200 ft. elevation (9 specimens, FMNH 144654); Rutaki Valley (Station 13) at 400 ft. elevation (6 specimens, FMNH 144600); Vaikapuangi Valley (Station 24), Mt. Maungaroa at 900 ft. elevation (10 specimens, FMNH 144639); summit of Mt. Te Kou (Station R-11) at 1,930 ft. elevation (3 specimens, FMNH 153388, FMNH 153413). "Cook Islands" (4 specimens, BPBM 167417).

*Remarks.*—Garrett (1881, p. 386) recognized that the Rarotonga shells were slightly different from the Atiu and Aitutaki populations (= *atiensis*), but did not give them nomenclatural recognition. In naming this species after W. Harper Pease, I am recognizing his early encouragement of Andrew Garrett and his description of many Pacific Island species.

The availability of many localized sets enabled using this species to establish patterns of variation for *Sinployea* and to provide criteria for judging interpopulational variation. As can be seen from Table XXI, even with only very small numbers of adults from different stations, there was only minor variability.

*Description of soft parts.*—Foot and tail elongated, slender, not tapering posteriorly, rounded behind. Sole undivided, without transverse corrugations. Pedal grooves high on foot, uniting across tail, suprapedal distinctly weaker. No caudal foot or caudal horn. Slime network rectangular, more prominent on tail than head. Foot truncated anteriorly, head extended well in front. Ommatophores long. Gonopore slightly behind and above right rhinophore.

Sole and tail yellow-white, head and neck with grayish suffusion. Eyespots black, stalk of ommatophores gray.

Mantle collar (MC) rather short and thick (fig. 42c), with a wide, even extension of mantle glands onto lung roof. Pneumostome a single opening masked on each side by swellings of mantle collar. Anus (A) opening above, but at same level anteriorly as external ureteric opening (KX). A deep-grooved urinary chamber (LK) leads into shallow groove from anus through mantle collar.

Pallial chamber (fig. 42c) extending  $\frac{1}{2}$  whorl apically. Lung roof with heavy concentrations of black speckles along principal pulmonary vein (HV) and mantle glands (MG), with secondary concentration near hindgut. Kidney (K) U-shaped, rectal lobe distinctly longer than pericardial, latter about twice as long as heart (H). Rectal lobe of kidney lapping completely under hindgut and onto parietal wall. Base of kidney extended backward between loop of intestine and outer wall covering, rounded. Ureter (KD) sigmoid, U-shaped,



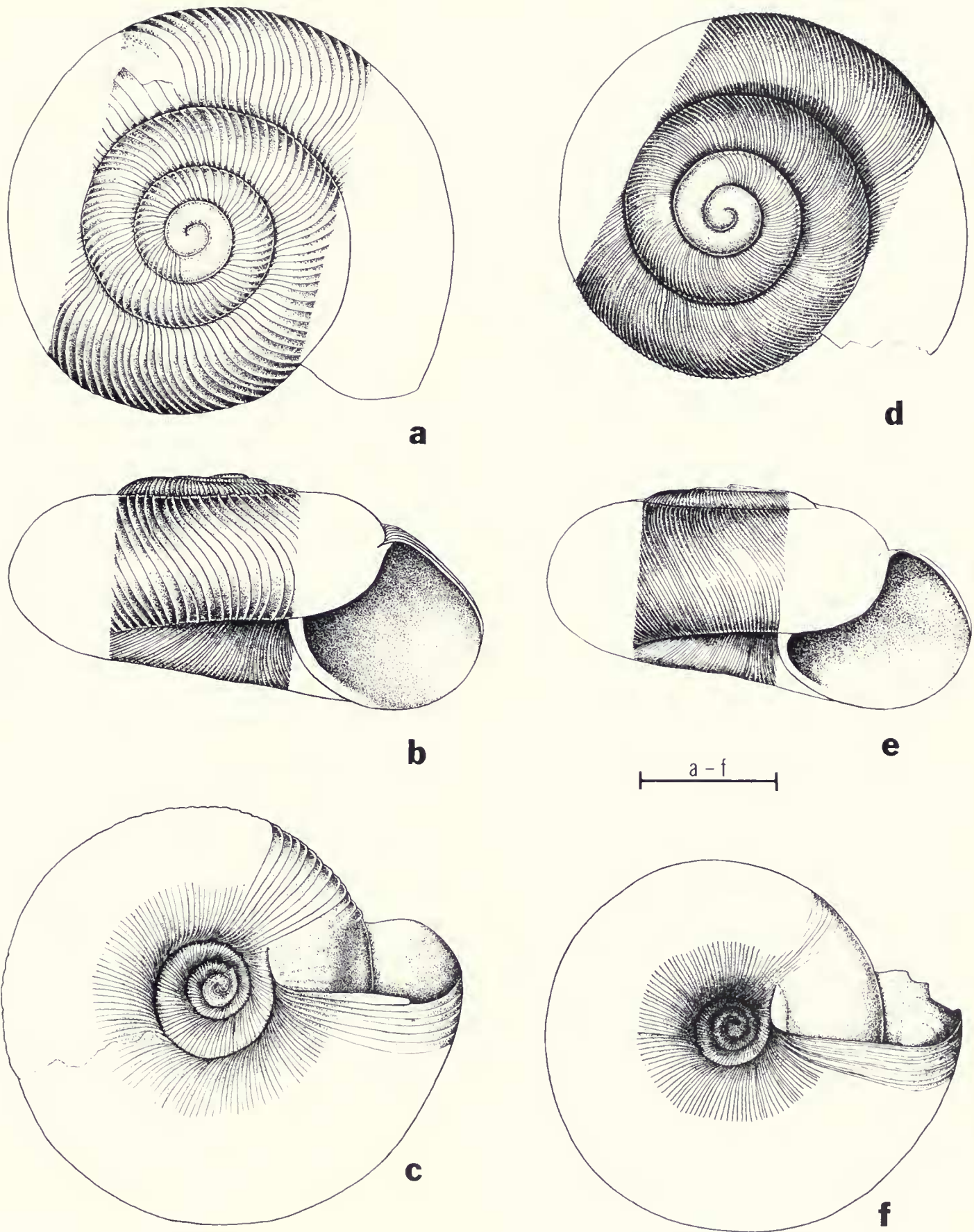


FIG. 45. a-c, *Sinployea peasei*, new species. Station 26, Mt. Maungaroa, 1,400 ft., Rarotonga, Cook Islands. Holotype. FMNH 155947; d-f, *Sinployea avanaensis*, new species. Station 18A, Upper Avana Valley, 600 ft, Rarotonga, Cook Islands. Holotype. FMNH 155948. Scale line equals 1 mm. (SH).

TABLE XXI. - LOCAL VARIATION IN SINPLOYEA PEASEI.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER
<u>peasei</u>					
FMNH 144547 (Sta. 4)	7	113.7±5.17 (93-130)	11.57±0.478 (9.78-13.24)	1.50±0.026 (1.38-1.58)	3.13±0.045 (3.03-3.36)
FMNH 144567 (Sta. 8)	5	109.8±7.10 (91-135)	11.08±0.366 (10.12-11.90)	1.47±0.043 (1.38-1.55)	3.16±0.148 (2.86-3.85)
FMNH 144664 (Sta. 30)	9	103.7±1.99 (96-116)	11.13±0.186 (10.30-11.89)	1.35±0.022 (1.25-1.45)	2.97±0.056 (2.66-3.16)
FMNH 144536 (Sta. 3)	7	108.3±2.15 (102-115)	10.97±0.182 (10.39-11.52)	1.52±0.058 (1.38-1.84)	3.14±0.058 (2.93-3.32)
FMNH 144639 (Sta. 24)	4	106.5±4.35 (95-115)	10.87±0.413 (9.99-11.59)	1.46±0.041 (1.38-1.58)	3.13±0.112 (2.89-3.42)
FMNH 144586 (Sta. 11)	8	106.5±3.37 (94-119)	10.79±0.352 (9.58-12.12)	1.55±0.055 (1.38-1.74)	3.15±0.033 (2.99-3.29)
FMNH 144652 (Sta. 28)	4	124.0±1.33 (100-155)	11.95±1.23 (8.80-14.16)	1.71±0.132 (1.45-1.84)	3.34±0.132 (3.09-3.65)
FMNH 144645 (Sta. 26)	28	110.1±3.07 (83-149)	11.55±0.309 (9.13-14.15)	1.84±0.020 (1.28-1.71)	3.10±0.032 (2.76-3.42)
FMNH 144600 (Sta. 13)	3	104.7±7.70 (96-120)	10.49±0.774 (9.39-11.98)	1.55±0.033 (1.51-1.61)	3.18±0.121 (3.03-3.32)
FMNH 144654 (Sta. 29)	5	127.2±15.54 (91-167)	12.35±0.842 (10.12-14.42)	1.62±0.094 (1.41-1.94)	3.24±0.222 (2.80-4.01)
FMNH 144578 (Sta. 10)	8	121.3±7.22 (92-156)	11.92±0.473 (10.35-14.66)	1.63±0.054 (1.41-1.84)	3.22±0.083 (2.83-3.52)
FMNH 144614 (Sta. 14)	26	114.5±2.00 (88-141)	11.90±0.209 (9.68-13.51)	1.51±0.020 (1.32-1.71)	3.08±0.030 (2.80-3.45)
BPBM 2331	7	-----	-----	1.88±0.070 (1.69-2.12)	3.61±0.070 (3.41-3.94)

	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO
Sta. 4	0.480±0.0062 (0.457-0.500)	4 3/8-(4 1/4-4 1/2)	0.76±0.021 (0.69-0.86)	4.11±0.059 (3.92-4.38)
Sta. 8	0.494±0.0154 (0.475-0.540)	4 1/4-(4 1/8-4 3/8)	0.79±0.045 (0.69-0.92)	4.00±0.092 (3.75-4.18)
Sta. 30	0.455±0.0075 (0.415-0.489)	4+(4-4 1/4)	0.73±0.025 (0.63-0.86)	4.06±0.081 (3.54-4.29)
Sta. 3	0.484±0.0154 (0.440-0.554)	4 1/4+(4 1/8-4 1/2)	0.80±0.035 (0.72-0.99)	3.94±0.1211 (3.26-4.21)
Sta. 24	0.469±0.0051 (0.458-0.478)	4 3/8-(4 1/4-4 1/2)	0.78±0.043 (0.69-0.86)	4.02±0.1411 (3.69-4.38)
Sta. 11	0.491±0.0145 (0.442-0.546)	4 3/8-(4 1/8-4 1/2)	0.79±0.015 (0.72-0.86)	3.97±0.050 (3.80-4.14)
Sta. 28	0.513±0.0186 (0.468-0.558)	4 5/8+(4 1/4-5 1/8)	0.88±0.068 (0.76-1.05)	3.83±0.138 (3.47-4.13)
Sta. 26	0.493±0.0049 (0.448-0.538)	4 3/8+(4 1/8-4 3/4)	0.81±0.017 (0.63-0.99)	3.88±0.057 (3.33-4.43)
Sta. 13	0.487±0.0235 (0.455-0.533)	4 3/8-(4 1/4-4 3/8)	0.86±0.038 (0.79-0.92)	3.72±0.090 (3.61-3.83)
Sta. 29	0.501±0.0065 (0.484-0.521)	4 1/2-(4 1/8-5 1/8)	0.85±0.109 (0.66-1.25)	3.92±0.200 (3.21-4.35)
Sta. 10.	0.506±0.0092 (0.463-0.535)	4 3/8-(4 1/4-4 1/2)	0.81±0.039 (0.66-1.02)	4.01±0.109 (3.45-4.50)
Sta. 114	0.492±0.0040 (0.447-0.533)	4 1/4+(4 1/8-4 1/2)	0.79±0.010 (0.66-0.89)	3.90±0.046 (3.52-4.60)
BPBM 2331	0.521±0.0166 (0.464-0.587)	4 5/8+(4 1/2-5)	0.99±0.038 (0.82-1.12)	3.65±0.144 (3.22-4.36)



evenly expanded, a strip of lung roof visible between arms of ureter. At anterior end of rectal kidney lobe, ureter passes alongside hindgut on lung roof forward to pneumostome. Heart (H) fairly large, angling slightly from parallel to hindgut. Principal pulmonary vein (HV) slender, flanked by black speckling, paralleling hindgut until anterior quarter of pallial cavity, then angling toward anus, finally reaching mantle glands. No conspicuous secondary venation.

Ovotestis (G) imbedded in first quarter whorl above stomach-intestine reflexion, consisting of a single clump of varyingly split finger-like lobes, internally with iridescent rods. First part of hermaphroditic duct (GD) a very thin collecting tubule, expanding to a slender, opaque iridescent tube for length of stomach to middle of albumen gland (GG), then narrowing to a sinuous narrow tube just before entering talon (GT). Albumen gland small, darker in color than prostate (DG), cradled between intestinal loops and base of kidney in body cavity just above and morphologically below apex of pallial cavity. Head of spermatheca (S) buried between base of albumen gland and head of prostate. Talon a slender tube with bulbously expanded head down to carrefour, hermaphroditic duct entering laterally on head of carrefour, which tapers from secondary expansion below apex to head of prostate-uterus. Prostate (DG) short, of large, white acini entering a groove in uterine wall. Uterus (UT) with 2 chambers, upper (UT<sub>1</sub>) a very thin-walled sac partly filled with spongy tissue, opening through a glandular collar into a lower chamber, white in color, with thick glandular walls, smooth except for 2 pilasters extending into muscular-walled free oviduct (UV).

Vas deferens (VD) from base of prostate at level of spermathecal stalk contraction, wide at first with internal pilasters, tapering down to a thin tube by level of penioviducal angle, passing up along penis, but not bound to it, until entering epiphallus (E). Latter a swollen muscular tube with internal longitudinal pilasters entering penis (P) through a small vergic papilla (PV, fig. 42e). Penial retractor (PR) arising on diaphragm near apex of pallial cavity, inserting in a U-fan around base of epiphallus. Penis proper about 1.1–1.3 mm. long, expanded apically with a minor constriction marking internal muscular collar, then tapering slowly to base of main glandular part, finally continuing as a slender tube to atrium. Internally (fig. 42d), penis with a cup-shaped vergic papilla (PV) surrounded by a muscular collar of 3 circular pilasters. Below this, a huge U-shaped muscular stimulatory pad occupies rest of penial bulge. Lower part and section between arms of "U" with walls longitudinally folded. Atrium (Y) fairly long, without distinctive internal sculpture.

Free oviduct (UV) a short tube with smooth muscular walls externally, internally with smooth glandular surface, opening into vagina (V) through a glandular collar. Spermatheca (S) and base of vagina swollen with glandular walls, tapering above to a slender stalk, then an oval head lying in angle between prostate and albumen gland. Vagina (V) long, swollen apically with glandular walls, lower part a narrow tube with weak pilasters.

Buccal mass and esophagus typical, white salivary glands uniting above esophagus. Stomach expanding just above apex of pallial cavity, extending  $\frac{3}{4}$  of a whorl apically, occupying parietal and most of palatal wall surfaces. About  $\frac{1}{3}$  of way from apex, stomach narrows from base, preparatory to stomach-intestine junction. First part of intestine angling down to columellar margin, running along this edge to apex of pallial cavity, looping up under kidney to near midpoint of whorl, reflexing backward for about twice its width, then turning up to parietal-palatal margin and forward as hindgut. Distance between apex of pallial cavity and stomach greatly reduced, loops of intestine very short, hindgut only reaching parietal-palatal angle at base of kidney.

Free retractor muscle system as in *Charopa coma*.

Enervation of penis from right cerebral ganglion.

(Based on FMNH 144645, several whole examples.)

***Sinployea avanaensis*, new species.** Figures 43a–e, 45d–f.

**Diagnosis.**—Shell rather large, diameter 2.86–3.82 mm. (mean 3.21 mm.), with  $3\frac{3}{4}$ – $4\frac{1}{2}$  normally coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion  $\frac{1}{6}$  to  $\frac{1}{5}$  of body whorl width, H/D ratio 0.427–0.516

(mean 0.474). Apical sculpture of about 10–14 very fine spiral cords, rarely distinct enough to be tallied. Postnuclear whorls with very fine and crowded, protractively sinuated, narrow radial ribs, 175–290 (mean 225.8) on the body whorl, whose interstices are less than twice their width. Ribs/mm. 16.28–25.06 (mean 20.82). Microsculpture of fine radial riblets, 2–4 between each pair of major ribs, barely visible spiral riblets and weak secondary spiral cording visible on upper surface and basal margins. Umbilicus narrow, V-shaped, last whorl decoiling more rapidly, contained 3.87–5.69 times (mean 4.78) in the diameter. Whorl contour typical, aperture a little more compressedly ovate than normal.

The extremely fine and crowded radial ribs, dark coloration, and narrower umbilicus effectively separate *Sinployea avanaensis* (fig. 45d–f) from *S. peasei* (fig. 45a–c). Other Rarotonga species are much larger and have fewer or reduced radial ribs. Of the extralimital species, only the much smaller *S. navutuensis* (fig. 68d–f) from Lau and *S. godeffroyana* (fig. 69a–c) from Viti Levu approach the rib spacing of *S. avanaensis*. No other *Sinployea* has more than 175 ribs on the body whorl.

**Description.**—Shell rather large, with slightly less than  $4\frac{1}{4}$  normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.510. Embryonic whorls 1½, sculpture of about 13 very fine spiral cords, somewhat worn. Postnuclear whorls with fine, narrow, very crowded, strongly protractively sinuated radial ribs, about 203 on the body whorl, whose interstices are no more than twice their width. Microsculpture of fine radial riblets, 2–4 between each pair of major ribs, crossed by barely visible spiral riblets, with a weak development of secondary spiral cording visible on the upper spire, becoming strong on shell base and in umbilicus. Sutures deep, whorls strongly rounded above, flatly rounded laterally above periphery, with distinctly flattened basal margin, umbilical margin strongly rounded. Umbilicus narrow, V-shaped, last whorl decoiling much more rapidly, contained 5.33 times in the diameter. Color dark reddish brown. Aperture compressedly ovate, slightly flattened laterally above periphery, distinctly flattened basally, inclined about 25° from shell axis. Height of holotype 1.61 mm., diameter 3.16 mm.

**Holotype.**—Cook Islands: Rarotonga, Station 18a, upper Avana Valley at 600 ft. elevation. Collected by Laurie Price on lichens and moss-covered branches in December, 1964. FMNH 155948.

**Range.**—Upper Avana Valley at 300–1,000 ft. elevation, Rarotonga, Cook Islands.

**Paratypes.**—Rarotonga: Avana Valley between 300 and 1,000 ft. elevation (Stations 18, 18a, 32a, R-13, R-16) under loose bark or fungus and in crevices on moss and lichen-covered tree trunks and branches up to 15 ft. above ground level (137 specimens, FMNH 144631–2, FMNH 144671, FMNH 153381, FMNH 153383–5).

**Remarks.**—At the lowest elevation (Station R-13, 300 ft.) specimens were found only 1–6 ft. above ground level, whereas at the higher stations examples were taken up to 15 ft. above the ground. Probably they move higher, but practical problems in collecting prevented determination of upper limits. All examples were taken in and under moss and lichens or under loose bark, except for a few from Station 18 that were found under dead wood on the ground. Conditions were quite dry at the time, and the latter occurrence may represent a partial retreat after moisture. Size and shape variation is minimal (table XX).

The very reduced apical sculpture, almost uniform color, very crowded and numerous radial ribs, much narrower umbilicus, and more compressedly ovate aperture immediately separate *S. avanaensis* from the common *S. peasei*. The latter has been taken in lower Avana Valley (Station 14) at about 300 ft. elevation. It is widely distributed on other parts of Rarotonga and has been found on the summit of Mt. Te Kou, which heads both Takuvaine and Avana Valleys. The two species are probably allopatric, with *S. peasei* living lower in Avana than *S. avanaensis*.

*Description of soft parts.*—Foot and tail as in *S. peasei*, length slightly less than shell diameter (fig. 43a). Sole undivided, pedal grooves uniting above tail, suprapedal distinctly weaker. No caudal horn, middorsal groove weak, slime network typical. Gonopore slightly behind and above right rhinophore. Body color yellow-white, with gray-black speckling on head and neck region. Mantle collar with tapered edge, a weak glandular extension onto pallial roof. Pneumostome shielded by a weak thickening of collar to form a right mantle lobe. Anus (A) and external ureteric pore (KX) opening at angle just inside pneumostome.

Pallial region (fig. 43b) extending apically  $\frac{1}{2}$  whorl, lung roof clear, without granules. Kidney (K) bilobed, rectal lobe distinctly longer and broader than pericardial, former lobe crossing hindgut to reach parietal wall, pericardial lobe about twice as long as heart. Apex tapering, U-shaped. Ureter (KD) complete, opening alongside anus, a strip of lung roof visible between ureter arms. Heart (H) almost parallel to hindgut, proportionately broad. Principal pulmonary vein (KV) angling toward pneumostome, without conspicuous lateral branches. Hindgut (HG) starting at apex of kidney, following parietal-palatal margin to anus.

Ovotestis (fig. 43c) occupying slightly less than  $\frac{1}{2}$  whorl above stomach reflexion, composed of 5–6 long, single or bifurcated, finger-like lobes lying parallel to whorl sides, merging irregularly near base. Hermaphroditic duct (GD) at first a very slender tubule, becoming abruptly swollen below stomach apex, iridescent until abruptly narrowing to reflex up albumen gland surface to base of talon. Albumen gland (GG) oval, deeply indented by head of spermatheca, intestinal loop, and digestive gland. Talon (GT) with circular head, hermaphroditic duct entering shaft just below head area, tapering to head of prostate-uterus. Prostate (fig. 43d) of long, finger-like acini, sometimes bifurcated, opening into a closed tube contained within uterine chamber. Uterus (UT) as in *S. peasei*.

Vas deferens (VD) wide and with glandular walls at first, narrowing before penioviducal angle, becoming a slender tube passing alongside penis to epiphallus. Latter an enlarged muscular tube with longitudinal pilasters, ending in a narrow neck before a muscular collar leading into penis. Penial retractor (PR) arising from diaphragm near pallial cavity apex, inserting in a U-shaped fan around base of epiphallus. Penis (P) about 1.4–1.6 mm. long, swollen on apical  $\frac{1}{2}$ – $\frac{3}{4}$ , a slight constriction marking end of muscular collar, lower  $\frac{1}{3}$ – $\frac{1}{2}$  a slender tube. Internally (fig. 43e) with a small verge (PV) nestled in a muscular collar generally containing two circular bands and followed by the typical doughnut cushion. Lower portion without distinctive sculpture. Atrium (Y) relatively long, equal in diameter to basal portion of penis, without special sculpture.

Free oviduct (UV) tapering, internally with glandular tissue and weak pilasters, opening above end of glandular zone in spermathecal region. Spermatheca (S) with head lying next to albumen gland, expanded near base with strong glandular zone that ends abruptly below junction with free oviduct. Vagina (V) tapering sharply after end of glandular zone, without special structures present.

Free muscle system as in *S. peasei*. Buccal retractors not split, esophagus typical. Stomach extending for  $\frac{3}{4}$  of a whorl, occupying normal position, expanding and narrowing abruptly. Intestinal loops compressed into  $\frac{1}{4}$  of a whorl between pallial cavity apex and stomach, tapered part of kidney extending well above much of loops. Digestive glands extending about  $1\frac{1}{2}$  whorls above ovotestis apex,

reduced to narrow strips along stomach, expanding in short area between stomach and kidney apex.

(Based on FMNH 144671, Station 32a, 4 adults, largest 3.49 mm. in diameter with  $4\frac{1}{4}$ + whorls.)

### *Sinployea proxima* (Garrett, 1872). Figure 46a–c.

*Pitya proxima* Garrett, 1872, Am. J. Conchol., 7 (4), p. 230, pl. 19.

fig. 24—common in several valleys on Rarotonga, Cook Islands.

*Patula proxima* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 386.

*Helix proxima* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 543.

*Helix (Patula) proxima* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 39, pl. 8, figs. 41–43.

*Endodonta (Charopa) proxima* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis.*—Shell relatively large, diameter 3.26–4.08 mm. (mean 3.61 mm.), with 4–4 $\frac{1}{4}$  normally coiled whorls. Apex and spire slightly to moderately and evenly elevated, rounded above, last whorl descending much more rapidly, spire protrusion about  $\frac{1}{4}$  body whorl width, H/D ratio 0.519–0.583 (mean 0.544). Apical sculpture of 12–15 very weak spiral ribs, usually too fine or worn for accurate counting. Postnuclear whorls with fine, narrow, prominent, strongly protractively sinuated radial ribs, 92–154 (mean 119.7) on the body whorl, often irregularly spaced, whose interstices usually are 2–3 times their width. Ribs/mm. 8.91–12.96 (mean 10.75). Microsculpture of fine radial riblets, 3–8 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Umbilicus narrow, U-shaped, last whorl decoiling slightly more rapidly, contained 4.48–6.16 times (mean 5.35) in the diameter, margins rounded. Whorl contours typical, sutures unique in distinct channeling after first postnuclear.

*Sinployea proxima* (fig. 46a–c) is immediately recognizable by its channeled suture. Its reduced apical sculpture and relatively narrow umbilicus separate it from most Rarotongan species. *Sinployea avanaensis* (fig. 45d–f) is similar in umbilical size, but has a normal suture, much more numerous and crowded radial ribs, and a distinctly more elevated spire.

*Description.*—Shell larger than average, with 4% moderately tightly coiled whorls. Apex and spire moderately elevated, rounded above, body whorl descending distinctly more rapidly, H/D ratio 0.557. Apical whorls 1%, sculpture eroded with traces of weak spiral ribs remaining. Postnuclear whorls with moderately prominent, very crowded, protractively sinuated radial ribs, 154 on the body whorl, whose interstices are about twice their width. Microsculpture of fine, radial riblets, 2–6 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, with a secondary sculpture of rather widely spaced spiral cords that become less distinct on body whorl. Sutures deeply channeled, whorls flatly rounded laterally above periphery and on basal margin. Color light yellow-horn with prominent, regular, reddish flammulations. Umbilicus narrow, U-shaped, slightly and regularly decoiling, contained 5.24 times in the diameter. Aperture ovate, flattened laterally above periphery and on basal margin, inclined about 20° from shell axis. Columellar and basal wall with moderate white callus. Height of lectotype 2.11 mm., diameter 3.79 mm.

*Lectotype.*—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47700.

*Range.*—Under stones and among rotting wood in several valleys on Rarotonga, Cook Islands.

*Paratypes.*—BPBM 2317, ANSP 47700.

*Material.*—Rarotonga (14 specimens, AMS, Zurich).



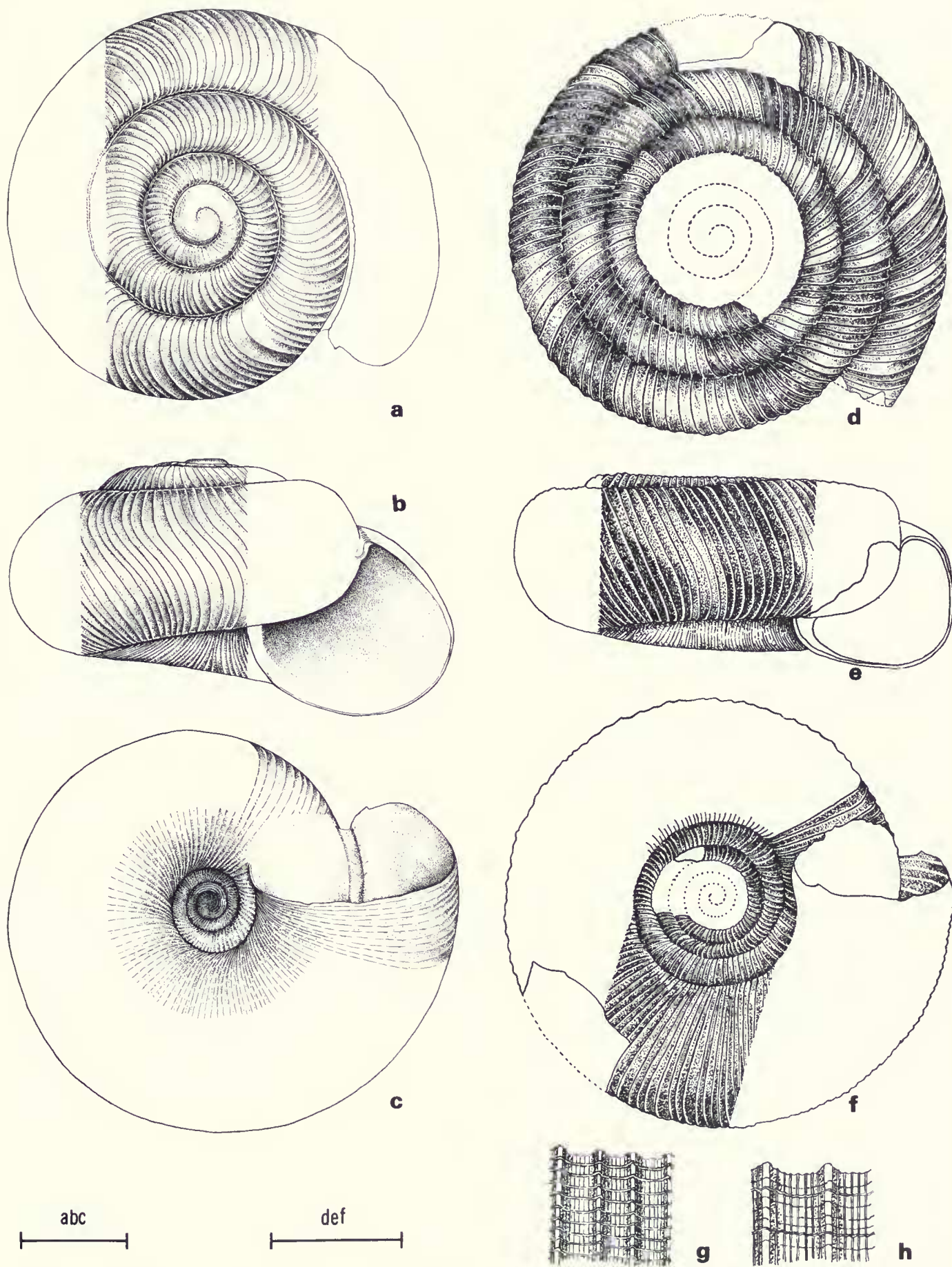


FIG. 46. **a-c**, *Sinployea proxima* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2317; **d-h**, *Sinployea planospira* (Garrett). **g-h**, Details of microsculpture. Rarotonga, Cook Islands. Lectotype. Zurich. Scale lines equal 1 mm. (**a-c**, SH; **d-h**, SG).

*Remarks.*—Although Garrett (1872, p. 230; 1881, p. 386) reported this as a "common" or "not uncommon" species found in several valleys, no additional material has been collected. The scattered Museum sets show clear indication of trading bias (table XX), with the BPBM residue of Garrett's personal collection containing the largest shells, the types in the ANSP only slightly smaller, and the specimens that eventually reached Mousson (now Zurich) and Hedley (AMS) noticeably smaller.

Channeling of the suture is relatively uncommon in the Pacific Basin endodontoids, being found elsewhere in the New Caledonian *Andrefrancia alveolus* (Gassies) (see Solem, 1961, pp. 454–456, fig. 12) and the Bismarck *Lagivala macroglyphis* (Rensch) (see p. 188). Ignoring the sutural alteration, *S. proxima* is only a slightly enlarged, more narrowly umbilicated derivative from the *peasei* stock.

#### *Sinployea planospira* (Garrett, 1881). Figure 46d–h.

*Patula planospira* Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 388—Rarotonga, Cook Islands.

*Helix (Patula) planospira* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 41.

*Endodonta (Charopa) planospira* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis.*—Shell relatively large, diameter 3.44–4.24 mm. (mean 3.74 mm.), with  $6\frac{1}{4}$ – $7\frac{1}{4}$  very tightly coiled whorls. Apex and early spire flat, body whorl descending rapidly, spire protrusion about  $\frac{1}{5}$ – $\frac{1}{4}$  body whorl width, H/D ratio 0.439–0.524 (mean 0.468). Apical sculpture eroded in available material, traces of spiral cording visible in one umbilicus. Postnuclear whorls with narrow, prominent, protractively sinuated radial ribs, 108–148 (mean 128.0) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 10.05–11.19 (mean 10.62). Microsculpture of fine radial riblets, 5–8 between each pair of major ribs, slightly finer and more crowded spiral riblets, and secondary spiral cording more clearly visible in umbilicus. Umbilicus widely open, cup-shaped, regularly decoiling, contained 2.75–2.98 times (mean 2.90) in the diameter, margins strongly rounded. Whorls strongly rounded above, flattened laterally and on basal margin.

*Sinployea planospira* (fig. 46d–h) has a wide umbilicus and much higher whorl count than any other Polynesian species. *Sinployea canalis* (fig. 49a–c) is much larger, has one whorl less, and a much less elevated spire, although it is very similar in rib count and umbilical proportions (table XIX).

*Description.*—Shell larger than average, with  $6\frac{1}{4}$  tightly coiled whorls. Apex and spire flat, body whorl descending slightly, H/D ratio 0.442. Embryonic whorls  $1\frac{1}{2}$ , sculpture mostly eroded, with traces of widely spaced spiral ribbing remaining. Postnuclear whorls with narrow, protractively sinuated radial ribs, 108 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of very fine radial ribs, 5–8 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets with a secondary sculpture of spiral cording developed in the umbilicus. Sutures deep, whorls strongly rounded above, flattened laterally and on basal margin. Umbilicus U-shaped, broadly open, regularly decoiling, contained 2.98 times in the diameter. Color light yellowish white with traces of irregularly spaced, broad, reddish maculations. Aperture subtriangular, strongly flattened laterally and on basal margin, inclined about  $15^\circ$  from the shell axis. Height of lectotype 1.51 mm., diameter 3.42 mm.

*Lectotype.*—Cook Islands: Rarotonga. Collected by Andrew Garrett. Zoologisches Museum der Universität

Zurich, Mousson collection ex Museum Godeffroy in 1882.

*Range.*—Rarotonga, Cook Islands.

*Paratypes.*—Rarotonga (2 specimens, Zurich).

*Remarks.*—Because the collections of the Museum Godeffroy were destroyed during World War II and Garrett (1881, p. 388) stated that all material of this species had been deposited in that collection, I had assumed that this was a lost species. The discovery of two shells in the Mousson collection at Zurich that had been obtained from the Museum Godeffroy in 1882 allowed recognition of this taxon. Although Mousson had attached a manuscript name "*rarotongensis*," I have no doubt as to their identity. A third shell, also obtained by Mousson from the Museum Godeffroy, was under the manuscript name "*ortospirata* Mousson." It is a gerontic individual. Unfortunately, the type specimen was damaged during handling, hence the figures have dotted lines indicating the upper whorls.

The high whorl count is unmatched by other Polynesian Charopidae and is much more similar to the pattern observed in the Endodontidae. Traces of apical sculpture are sufficiently clear to leave no doubt as to its affinities. Only *S. canalis* of the Rarotongan species has the umbilicus as widely open. Differences are given in the diagnosis.

#### *Sinployea rudis* (Garrett, 1872). Figure 47d–f.

*Pitys rudis* Garrett, 1872, Am. J. Conchol., 7 (4), pp. 227–228, pl. 19, fig. 18—several valleys on Rarotonga, Cook Islands.

*Patula rudis* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 387.

*Patula sublaminate* "Mousson" Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 94—Nude name, tentatively synonymized by Garrett (1881).

*Helix rudis* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 547.

*Helix (Patula) rudis* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, pp. 39–40, pl. 8, figs. 44–46.

*Endodonta (Charopa) rudis* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis.*—Shell large, diameter 3.68–4.83 mm. (mean 4.04 mm.), with  $3\frac{3}{8}$ – $4\frac{1}{8}$  normally coiled whorls. Apex flat, spire moderately and evenly elevated, last whorl descending slightly more rapidly, spire protrusion more than  $\frac{1}{6}$  body whorl width, H/D ratio 0.500–0.642 (mean 0.553). Apical sculpture of 8–12 (mean 10.02) spiral cords and weak radial corrugations. Postnuclear sculpture of low, narrow, rather widely spaced protractive radial ribs on upper spire, becoming reduced and very irregular early on body whorl, absent near aperture. Microsculpture of fine radial riblets, crossed by finer and more crowded spiral riblets, reduced on body whorl. Umbilicus narrow internally, V-shaped, body whorl decoiling much more rapidly, contained 4.18–5.62 times (mean 4.87) in the diameter, margins rounded. Whorls flattened and indented laterally above periphery, producing a distinct suprapерipheral sulcus, strongly rounded on lower margins, aperture inclined about  $35^\circ$  from shell axis.

In having a suprapерipheral sulcus and losing major ribbing on the lower spire and body whorl, *Sinployea rudis* is quite distinctive among Polynesian species.

*Description.*—Shell relatively large, with slightly more than  $4\frac{1}{4}$  loosely coiled whorls. Apex and spire slightly but evenly elevated, body whorl descending more rapidly, H/D ratio 0.531. Apical whorls



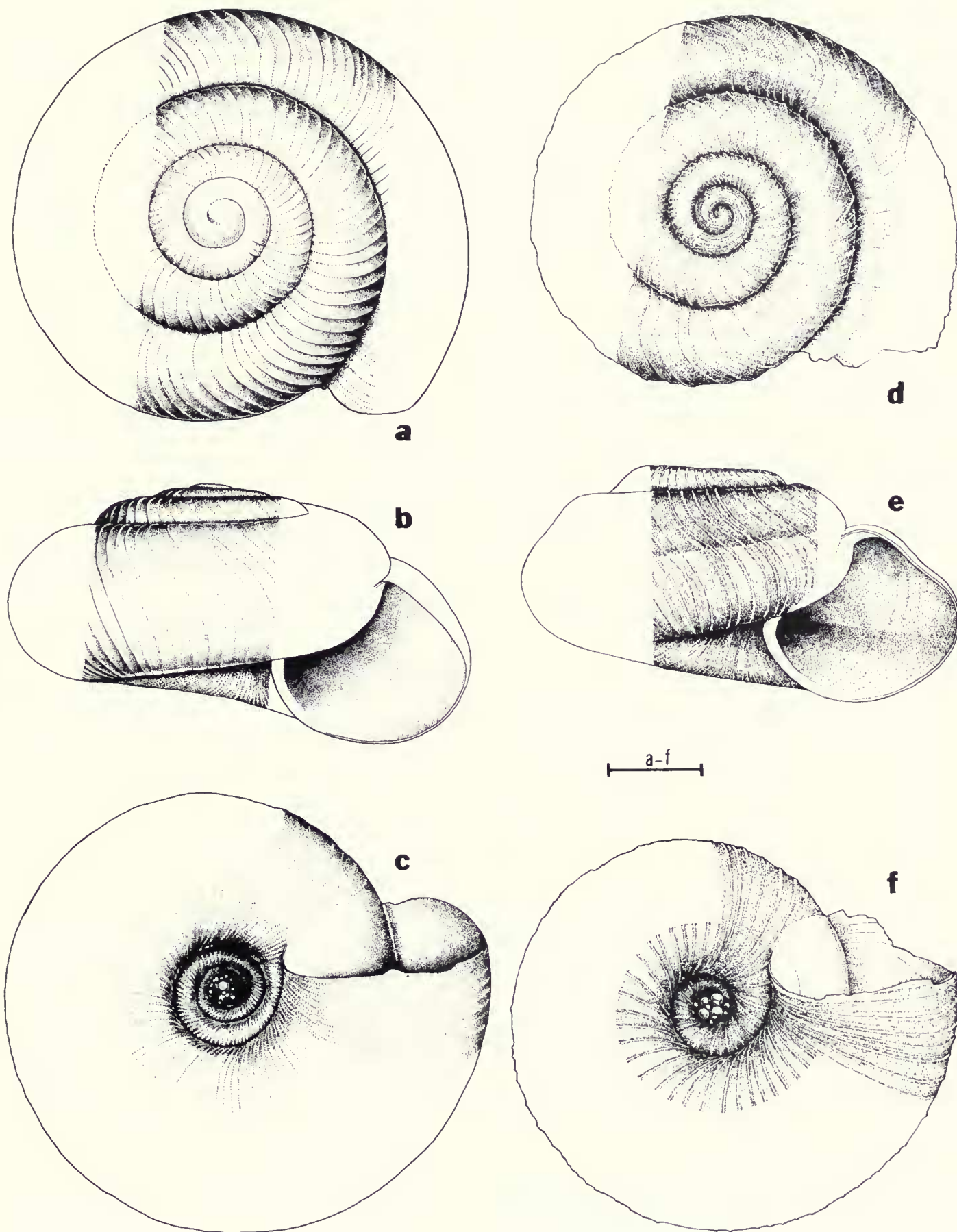


FIG. 47. **a-c**, *Sinployea decorticata* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2313; **d-f**, *Sinployea rudis* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2320. Scale line equals 1 mm. (*a-c*, SH; *d-f*, MM).

1½, sculpture of 11 prominent spiral ribs with a secondary microsculpture of radial and spiral riblets. Postnuclear whorls with narrow, low, irregular, protractively sinuated radial ribs, becoming greatly reduced or absent on the body whorl. Microsculpture of fine and somewhat irregular radial riblets crossed by distinctly finer and more crowded spiral riblets that are visible only at 96× magnification under strong lighting. Sutures deep, whorls shouldered above, flattened to indented laterally above periphery with gently rounded basal margin. Color greenish yellow-horn with extensive irregular reddish flammulations. Umbilicus narrow, V-shaped, regularly decoiling, aperture contained 5.42 times in the diameter. Height of lectotype 2.27 mm., diameter 4.28 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47701.

*Range*.—Several valleys on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2320, ANSP.

*Material*.—Cook Islands (9 specimens, BPBM 167420, FMNH 93820, FMNH 108559): Rarotonga (20 specimens, BPBM 167421, FMNH 46267, ANSP 47701).

*Remarks*.—Garrett (1881, p. 387) indicated that *Sinployea rudis* was common and that "we gathered hundreds in several valleys." In its flat spire, reduced sculpture, and very prominent supraperipheral sulcus, *S. rudis* is immediately separable from the other Rarotongan species.

The size difference between the type set and BPBM material (table XXIII) undoubtedly reflects retention of large specimens by Garrett.

### *Sinployea decorticata* (Garrett, 1872). Figure 47a–c.

*Pitys decorticata* Garrett, 1872, Am. J. Conchol., 7 (4), p. 228, pl. 19, fig. 19—a mountain ravine on Rarotonga, Cook Islands.

*Patula decorticata* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 387.

*Helix decorticata* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 542.

*Helix (Patula) decorticata* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 40, pl. 8, figs. 47–49.

*Endodonta (Charopa) decorticata* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 3.71–5.10 mm. (mean 4.30 mm.), with 4¾–5 normally coiled whorls. Apex and spire moderately to strongly elevated, body whorl descending more rapidly, spire protrusion about ½ body whorl width, H/D ratio 0.488–0.590 (mean 0.550). Apical sculpture of 8–10 (mean 9.0) fairly prominent spiral cords. Postnuclear whorls with high, thin, prominent, protractively sinuated and widely spaced radial ribs, 62–103 (mean 75.0) on the body whorl, whose interstices are 3–4 times their width. Ribs/mm. 4.84–6.47 (mean 5.61). Microsculpture of very fine radial riblets, 10–20 between each pair of major ribs, crossed by even finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 3.75–5.92 times (mean 4.32) in the diameter, margins rounded. Whorl contours and aperture typical.

*Sinployea decorticata* (fig. 47a–c) is more elevated and has fewer ribs and double the number of microradial riblets found in *S. otareae* (fig. 50a–c). *Sinployea tenuicostata* (fig. 50d–f) is larger, more depressed, has fewer ribs, and a flat spire. Other Rarotongan species differ in their finer and more crowded ribbing.

*Description*.—Shell very large, with 4¾ normally coiled whorls. Apex and spire moderately elevated, body whorl descending a little more rapidly, H/D ratio 0.528. Apical whorls 1¾, sculpture of 8 prominent spiral ribs, microsculpture obscured. Postnuclear whorls with low, rounded, protractively sinuated radial ribs, 73 on the body whorl, whose interstices are 3–4 times their width. Microsculpture occasionally visible as fine radial riblets, 10–20 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls flattened laterally above periphery and on basal margin. Color mainly leached from shell with traces of reddish flammulations remaining. Umbilicus moderately open, U-shaped, slightly and regularly decoiling, contained 3.84 times in the diameter. Aperture subcircular, flattened laterally above periphery and on basal margin, inclined about 20° from the shell axis. Height of lectotype 2.47 mm., diameter 4.67 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47754.

*Range*.—One mountain ravine on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2313, ANSP.

*Material*.—Rarotonga (17 specimens, BPBM 2313, BPBM 167422, ANSP 47754, SMF 165709, FMNH, NMWC).

*Remarks*.—Although Garrett (1881, p. 387) considered *Sinployea decorticata* and *S. otareae* to be "varieties" of one species, the differences in sculpture and shape (table XXIII) are sufficient to maintain specific separation. The two species were restricted to separate valleys "about three miles apart" (Garrett, 1881, p. 387).

### *Sinployea harveyensis* (Garrett, 1872). Figure 48a–c.

*Pitys harveyensis* Garrett, 1872, Am. J. Conchol., 7 (4), p. 228, pl. 19, fig. 20—common on Rarotonga, Cook Islands.

*Patula harveyensis* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 387.

*Helix harveyensis* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 542.

*Helix (Patula) harveyensis* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 40, pl. 8, figs. 51–53.

*Endodonta (Charopa) harveyensis* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 3.91–5.23 mm. (mean 4.35 mm.), with 4¾–5 normally coiled whorls. Apex and spire rather strongly elevated, slightly rounded above, body whorl descending more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.475–0.641 (mean 0.550). Apical sculpture of fine spiral cords, eroded or too faint to count accurately. Postnuclear whorls with fine, irregular, closely spaced, protractively sinuated radial ribs, too crowded and irregular to count on body whorl, whose interstices are often less than their width near aperture. Microsculpture visible on upper spire as very fine radial riblets, 3–7 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Umbilicus rather narrow, U-shaped, regularly decoiling, contained 3.65–5.48 times (mean 4.73) in the diameter, margins rounded. Whorls somewhat flattened laterally above periphery, very slightly on basal margin.

*Sinployea harveyensis* (fig. 48a–c) is characterized by its crowded, irregular major radial ribs and elevated spire. *Sinployea youngi* (fig. 48d–f) has a wider umbilicus, lower spire, more depressed shape, and less crowded radial ribbing (table XIX).



TABLE XXII. — LOCAL VARIATION IN COOK ISLAND SINPLOYEA, II.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>planospira</u>					
Zurich	3	128.0±20.02 (108–148)	1.77±0.226 (1.52–2.22)	3.74±0.250 (3.44–4.24)	0.468±0.0277 (0.439–0.524)
<u>youngi</u>					
Zurich	3	102.0±3.05 (96–106)	2.02±0.119 (1.85–2.25)	4.06±0.154 (3.77–4.30)	0.497±0.0139 (0.476–0.523)
BPBM 2315	4	127.8±7.43 (107–139)	2.47±0.098 (2.28–2.68)	4.76±0.117 (4.57–5.10)	0.518±0.0135 (0.493–0.553)
ANSP 47703	3	117.7±2.33 (114–122)	2.38±0.066 (2.32–2.52)	4.93±0.077 (4.80–5.07)	0.483±0.0156 (0.457–0.510)
<u>harveyensis</u>					
ANSP 47756	10	-----	2.19±0.045 (1.92–2.35)	4.12±0.033 (3.91–4.27)	0.531±0.0092 (0.475–0.572)
Zurich	4	-----	2.31±0.021 (2.25–2.35)	4.21±0.076 (4.11–4.44)	0.548±0.0065 (0.530–0.560)
BPBM 2343, BPBM 167423	8	REDUCED	2.64±0.077 (2.32–3.01)	4.71±0.111 (4.37–5.23)	0.561±0.0085 (0.530–0.604)
<u>canalis</u>					
Zurich, AMS	4	117.3±8.50 (98–133)	2.03±0.068 (1.85–2.15)	4.52±0.151 (4.17–4.90)	0.449±0.0055 (0.439–0.464)
ANSP 47752	5	122.0±12.23 (106–146)	2.09±0.055 (1.89–2.19)	4.62±0.156 (4.04–4.90)	0.452±0.0103 (0.427–0.481)
BPBM 2328	5	120.8±5.46 (107–130)	2.28±0.119 (2.02–2.65)	4.72±0.197 (4.40–5.50)	0.484±0.0170 (0.446–0.544)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>planospira</u>					
Zurich		6 5/8(6 1/4–7 1/4)	1.28±0.076 (1.15–1.41)	2.90±0.075 (2.75–2.98)	-----
<u>youngi</u>					
Zurich		4+(4–4 1/4)	1.04±0.016 (1.02–1.09)	3.87±0.098 (3.68–4.00)	11.33±0.34 (11–12)
BPBM		4 1/2–(4 3/8–4 5/8)	1.34±0.097 (1.15–1.61)	3.57±0.190 (3.15–4.06)	10.25±0.25 (10–11)
ANSP		4 3/4+(4 1/2–5)	1.33±0.115 (1.12–1.51)	3.75±0.323 (3.33–4.39)	10.67±0.66 (10–12)
<u>harveyensis</u>					
ANSP		4 1/2+(4 3/8–4 7/8)	0.89±0.031 (0.79–1.12)	4.61±0.136 (3.65–5.08)	-----
Zurich		4 1/2(4 1/4–4 5/8)	0.86±0.056 (0.76–1.02)	4.89±0.240 (4.32–5.48)	-----
BPBM		4 7/8–(4 5/8–5 1/8)	0.99±0.039 (0.82–1.18)	4.77±0.156 (4.11–5.29)	-----
<u>canalis</u>					
Zurich		4 3/4+(4 1/2–5 1/8)	1.53±0.064 (1.38–1.68)	2.93±0.030 (2.87–3.00)	10.25±0.25 (10–11)
ANSP		5–(4 5/8–5 1/4)	1.63±0.076 (1.38–1.84)	2.83±0.054 (2.64–2.96)	9.60±0.60 (8–11)
BPBM		5+(4 3/4–5 1/2)	1.61±0.079 (1.41–1.84)	2.97±0.067 (2.73–3.10)	10.80±0.49 (9–12)

*Description.*—Shell very large, with 4% normally coiled whorls. Apex and spire slightly elevated, body whorl descending a little more rapidly, H/D ratio 0.524. Apical whorls 1%, sculpture mainly eroded with traces of spiral ribbing remaining. Postnuclear whorls with low, rounded, irregularly spaced, protractively sinuated radial ribs, becoming indistinct on body whorl. Microsculpture a lattice of coequal radial and spiral riblets. Sutures moderately impressed, whorls flat-

tened laterally above periphery and on basal margin. Color light yellow-horn with widely spaced, reddish markings absent on base of shell. Umbilicus U-shaped, relatively narrow, regularly decoiling, contained 4.66 times in the diameter. Aperture ovate, flattened laterally above periphery and slightly on basal margin, inclined about 20° from the shell axis. Height of lectotype 2.17 mm., diameter 4.14 mm.

TABLE XXIII. - LOCAL VARIATION IN COOK ISLAND SINPLOYEA, III.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>rudis</u>					
ANSP 47701	10	-----	2.12±0.047 (1.85-2.32)	3.95±0.049 (3.71-4.30)	0.537±0.0085 (0.500-0.575)
BPBM 2320, BPBM 167420	6	-----	2.44±0.088 (2.28-2.85)	4.26±0.135 (3.94-4.83)	0.574±0.0165 (0.520-0.642)
<u>decorticata</u>					
BPBM 2313	6	89.5±13.54 (76-103)	2.41±0.118 (2.19-2.98)	4.29±0.170 (3.94-5.10)	0.562±0.0118 (0.520-0.590)
BPBM 47754	4	73	2.53±0.051 (2.45-2.68)	4.63±0.079 (4.44-4.80)	0.547±0.0090 (0.528-0.566)
<u>otareae</u>					
BPBM 167418-9	8	-----	2.34±0.083 (2.07-2.63)	4.57±0.084 (4.38-4.90)	0.511±0.0097 (0.474-0.540)
BPBM 2335	7	107.0±5.87 (96-116)	2.54±0.092 (2.25-2.98)	4.80±0.097 (4.47-5.23)	0.529±0.0136 (0.479-0.570)
ANSP 47755	8	92.29±3.76 (81-110)	2.45±0.039 (2.32-2.65)	4.83±0.065 (4.54-5.00)	0.507±0.0088 (0.470-0.555)
<u>tenuicostata</u>					
ANSP 47702	2	46.0±1.00 (45-47)	2.04±0.083 (1.95-2.12)	4.14±0.033 (4.11-4.17)	0.491±0.0163 (0.475-0.508)
Zurich	3	47.7±1.20 (46-50)	2.33±0.040 (2.25-2.38)	4.55±0.192 (4.20-4.87)	0.513±0.0133 (0.489-0.535)
BPBM 2325	5	51.4±3.65 (43-65)	2.46±0.049 (2.38-2.65)	4.96±0.171 (4.44-5.46)	0.499±0.0170 (0.437-0.537)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>rudis</u>					
ANSP	4	1 1/4-(3 7/8-4 3/8)	0.80±0.016 (0.76-0.92)	4.90±0.111 (4.18-5.42)	10.43±0.31 (9-12)
BPBM	4	3/8+(4 1/4-4 5/8)	0.88±0.048 (0.79-1.12)	4.83±0.143 (4.30-5.17)	9.00±0.58 (8-10)
<u>decort.</u>					
BPBM	4	5/8+(4 3/8-5)	0.90±0.036 (0.79-1.02)	4.77±0.257 (4.20-5.92)	8.50±0.50 (8-9)
BPBM	4	3/4(4 1/2-5)	1.13±0.044 (1.02-1.22)	4.06±0.099 (3.84-4.32)	8
<u>otareae</u>					
BPBM	4	5/8+(4 1/2-5)	1.11±0.031 (1.02-1.25)	4.11±0.051 (3.92-4.29)	10.00±0.46 (8-12)
BPBM	4	7/8(4 3/4-5)	1.22±0.036 (1.09-1.35)	3.91±0.061 (3.71-4.22)	9.29±0.42 (8-11)
ANSP	4	3/4+(4 1/2-5)	1.16±0.064 (0.89-1.41)	4.24±0.230 (3.47-5.52)	8.87±0.40 (8-11)
<u>tenuico.</u>					
ANSP	4	(3 7/8-4 1/8)	0.82±0.033 (0.79-0.86)	5.01±0.240 (4.77-5.25)	11.50±0.50 (11-12)
Zurich	4	1/8(4-4 1/4)	0.84±0.040 (0.79-0.92)	5.35±0.087 (5.25-5.52)	10.00±0.58 (9-11)
BPBM	4	3/8-(4-4 1/2)	1.00±0.074 (0.82-1.18)	5.02±0.327 (4.29-6.20)	10.00±0.32 (9-11)



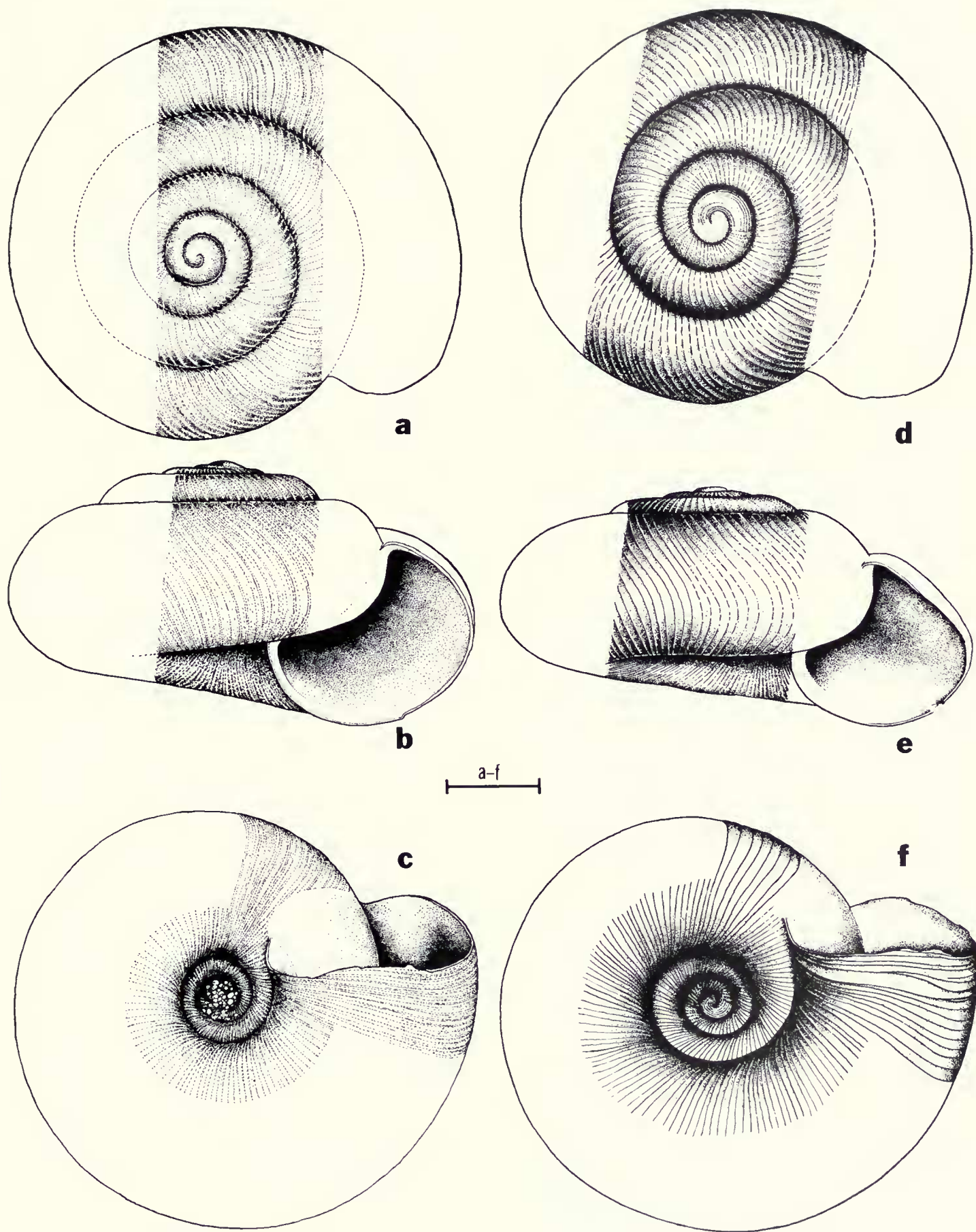


FIG. 48. **a–c**, *Sinployea harveyensis* (Garrett). Rarotonga, Cook Islands. Lectotype. BPBM 2343; **d–f**, *Sinployea youngi* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2315. Scale line equals 1 mm. (*a–c*, MM; *d–f*, SH).

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47756.

*Range*.—Common on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2343, ANSP.

*Material*.—Rarotonga (20 specimens, BPBM 167423, ANSP 47756, FMNH 46258, Zurich).

*Remarks*.—Garrett did not state whether *Sinployea harveyensis* was widely distributed or restricted in its habitat "under rotten wood" (Garrett, 1872, p. 228). Usually he specified if only a single valley was involved. I suspect that *S. harveyensis* had a wide range on the island. The very fine radial sculpture is similar to that seen in the Society Island *Sinployea*, but *S. harveyensis* lacks the prominent periostracal extensions that characterize the former. Garrett's retention of large examples is very clearly shown in Table XXII.

### *Sinployea youngi* (Garrett, 1872). Figure 48d–f.

*Pityis youngi* Garrett, 1872, Am. J. Conchol., 7 (4), p. 229, pl. 19, fig. 22—a single valley on Rarotonga, Cook Islands.

*Patula youngi* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 388.

*Helix youngi* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 543.

*Helix (Patula) youngi* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 40, pl. 8, figs. 54–56.

*Endodonta (Charopa) youngi* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 3.75–5.07 mm. (mean 4.54 mm.), with  $3\frac{1}{2}$ –5 loosely coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion about  $\frac{1}{2}$  body whorl width, H/D ratio 0.457–0.553 (mean 0.499). Apical sculpture of 10–12 (mean 10.73) prominent spiral cords. Postnuclear whorls with prominent, large, protractively sinuated radial ribs, 96–139 (mean 115.4) on the body whorl, whose interstices are about twice their width. Ribs/mm. 7.15–9.68 (mean 8.13). Microsculpture of fine radial riblets, 3–6 between each pair of major ribs, crossed by slightly lower and equally crowded spiral riblets. No secondary spiral cording visible. Umbilicus widely open, V-shaped, last whorl decoiling more rapidly, contained 3.15–4.39 times (mean 3.73) in the diameter, margins rounded. Whorls strongly flattened laterally above periphery and slightly on basal margin.

*Sinployea youngi* (fig. 48d–f) is very similar to *S. harveyensis* (fig. 48a–c) but differs in its more depressed shape, lower spire, wider umbilicus, and less crowded ribbing. *Sinployea canalis* (fig. 49a–c) has a much wider umbilicus, much more depressed shape, greater whorl count, and more laterally compressed whorl contour. Other species from Rarotonga differ most obviously in their more widely spaced ribbing or much smaller size.

*Description*.—Shell very large, with  $4\frac{1}{2}$  relatively loosely coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending more rapidly, H/D ratio 0.510. Apical whorls  $1\frac{1}{2}$ , sculpture of 10 prominent spiral cords, microsculpture obscured. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, about 117 on the body whorl where they become slightly irregular, whose interstices are 3–5 times their width. Microsculpture a lattice of very fine radial riblets, 3–6 between each pair of major ribs, and slightly smaller, more crowded, spiral riblets. Sutures moderately impressed, whorls flattened laterally above periphery and basally. Color dark reddish purple-brown. Umbilicus V-shaped, moderately open, regularly decoiling, contained 4.39

times in the diameter. Aperture ovate, strongly flattened laterally above periphery and basally, inclined about  $20^\circ$  from the shell axis. Height of lectotype 2.50 mm., diameter 4.91 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47703.

*Range*.—One valley on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2315, ANSP.

*Material*.—Rarotonga (13 specimens, ex BPBM 2339, FMNH 46502, Zurich).

*Remarks*.—Although reported as being collected "in one valley, the habitat of the typical *decorticata*" (Garrett, 1881, p. 388), it was not specified if the species were sympatric or allopatric. *Sinployea decorticata* has fewer and much more widely spaced radial ribs and a more elevated spire than does *S. youngi*. *Sinployea harveyensis* is more similar, but has the apical cords reduced and the radial ribbing quite crowded and irregular on the body whorl besides differing in proportions (table XXII).

*Sinployea youngi* was "A somewhat rare species. . . . On the ground in damp woods" (Garrett, 1872, p. 229).

### *Sinployea canalis* (Garrett, 1872). Figure 49a–c.

*Pityis canalis* Garrett, 1872, Am. J. Conchol., 7 (4), p. 227, pl. 19, fig. 17—one valley on Rarotonga, Cook Islands.

*Patula canalis* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 385.

*Helix canalis* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 546.

*Helix (Patula) canalis* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 39, pl. 8, figs. 38–40.

*Endodonta (Charopa) canalis* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 4.01–5.46 mm. (mean 4.63 mm.), with  $4\frac{1}{2}$ – $5\frac{1}{2}$  tightly coiled whorls. Apex and early spire flat or barely elevated, lower spire descending slightly, body whorl descending sharply, spire protrusion about  $\frac{1}{10}$  body whorl width, H/D ratio 0.427–0.544 (mean 0.463). Apical sculpture of 8–12 (mean 10.21) prominent spiral cords. Postnuclear whorls with fine, narrow, rather closely spaced, protractively sinuated radial ribs, 98–146 (mean 119.8) on the body whorl, whose interstices are 3–4 times their width. Ribs/mm. 7.07–9.74 (mean 8.22). Microsculpture of rather widely spaced radial riblets, 3–5 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Occasionally weak secondary spiral cording visible in umbilicus and sutures. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.64–3.10 times (mean 2.91) in the diameter. Sutures very deep, whorls shouldered above, nearly vertically compressed on outer margin, basal margin strongly rounded, aperture inclined about  $25^\circ$  from shell axis.

The widely open umbilicus, strongly laterally compressed whorls, fine ribbing, and large size characterize *Sinployea canalis* (fig. 49a–c). Other Cook Island species of similar size have much more widely spaced ribbing and narrower umbilici (*S. otareae*, fig. 50a–c, and *S. tenuicostata*, fig. 50d–f) or normally contoured whorls and a narrower umbilicus (*S. youngi*, fig. 48d–f). The slightly larger Samoan *S. complementaria* (fig. 56a–f) has a much narrower umbilicus, fewer and more widely spaced radial ribs, and many more micro-radial riblets.

*Description*.—Shell very large, with slightly less than  $5\frac{1}{4}$  rather tightly coiled whorls. Apex and spire slightly sunken, body whorl



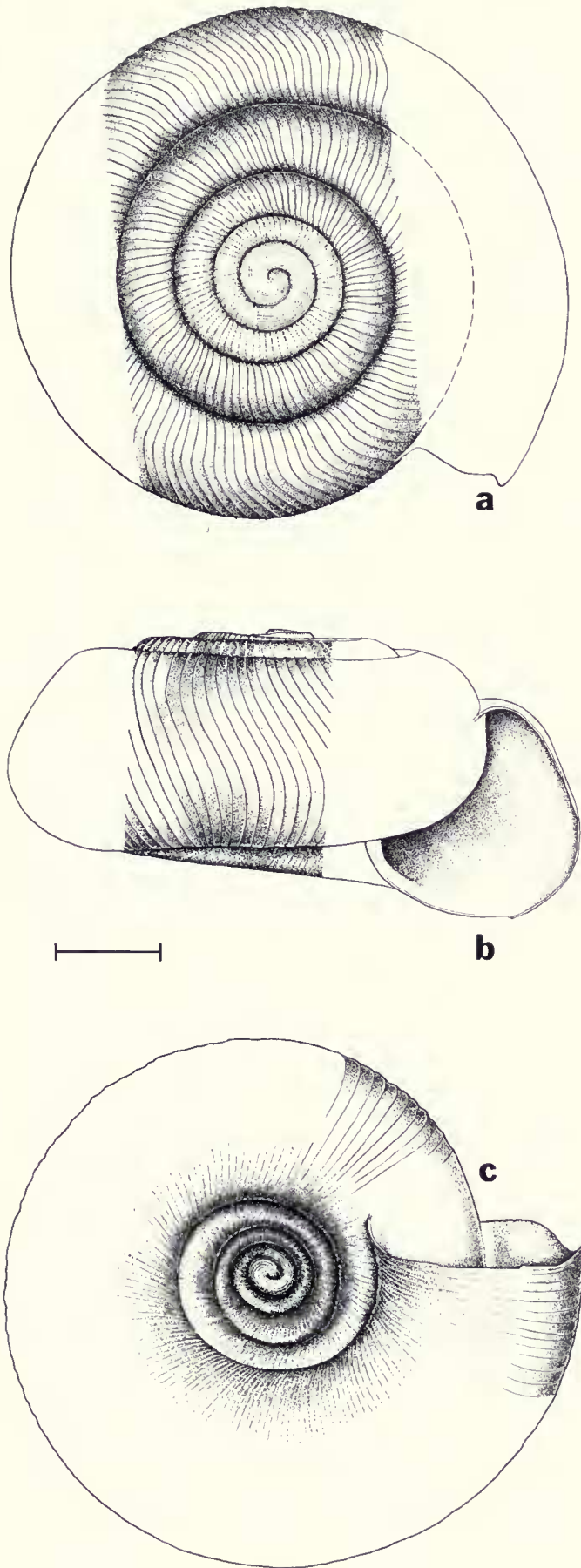


FIG. 49. a-c, *Sinployea canalis* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2328. Scale line equals 2 mm. (SH).

descending moderately, H/D ratio 0.427. Apical whorls 1%, sculpture of 8 prominent spiral ribs with a barely visible radial microsculpture. Postnuclear whorls with low, rounded, relatively crowded, protractively sinuated radial ribs, 106 on the body whorl, whose interstices are 2–3 times their width. Microsculpture a lattice of fine radial riblets, 3–5 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets with a secondary sculpture of spiral cording visible in suture and umbilicus. Sutures deep, whorls shouldered above, flattened laterally above periphery and on basal margin. Color yellowish horn with extensive vague reddish flammulations. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.96 times in the diameter. Aperture subovate, strongly flattened laterally above periphery and on basal margin, inclined about 25° from the shell axis. Height of lectotype 2.07 mm., diameter 4.77 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47752.

*Range*.—One valley on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2328, ANSP.

*Material*.—Rarotonga (13 specimens, AMS, Zurich, SMF 165456).

*Remarks*.—The strong lateral compression of the body whorl is not duplicated by any of the other Polynesian species and provides a strong contrast (fig. 49b) to the other Rarotongan species. Garrett (1872, p. 227) recorded this as a "somewhat rare species, found on the ground in damp forests, and confined to a single valley." Measured sets (table XXII) show very little variation and suggest fractions of a single population.

#### *Sinployea otareae* (Garrett, 1872). Figure 50a–c.

*Pitya otareae* Garrett, 1872, Am. J. Conchol., 7 (4), pp. 228–229, pl. 19, fig. 21—one valley on Rarotonga, Cook Islands.

*Patula otareae* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 94.

*Helix otareae* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 543.

*Patula decorticata* var. *otareae* (Garrett), Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 387.

*Helix (Patula) decorticata* var. *otareae* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 40, pl. 8, fig. 50.

*Endodonta (Charopa) decorticata* var. *otareae* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 4.21–5.20 mm. (mean 4.68 mm.), with 4½–5 relatively tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion more than ¼ body whorl width, H/D ratio 0.470–0.570 (mean 0.516). Apical sculpture of 8–12 (mean 9.41) prominent spiral cords. Postnuclear whorls, with narrow, prominent, protractively sinuated, rather widely spaced radial ribs, 81–116 (mean 95.6) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 5.72–7.73 (mean 6.48). Microsculpture of fine, crowded radial riblets, 6–10 between each pair of major ribs, crossed by finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus open, V-shaped, regularly decoiling, contained 3.47–5.52 times (mean 4.10) in the diameter, margins rounded. Whorl contours and aperture typical.

The presence of only six to ten microradials between each pair of major ribs at once separates *Sinployea otareae* (fig. 50a–c) from *S. decorticata* (fig. 47a–c). Individual specimens may show the size and shape characters of the other species, but the sculptural difference is consistent. *Sinployea tenuicostata* (fig. 50d–f) has a flat spire, fewer ribs, and a narrower umbilicus.

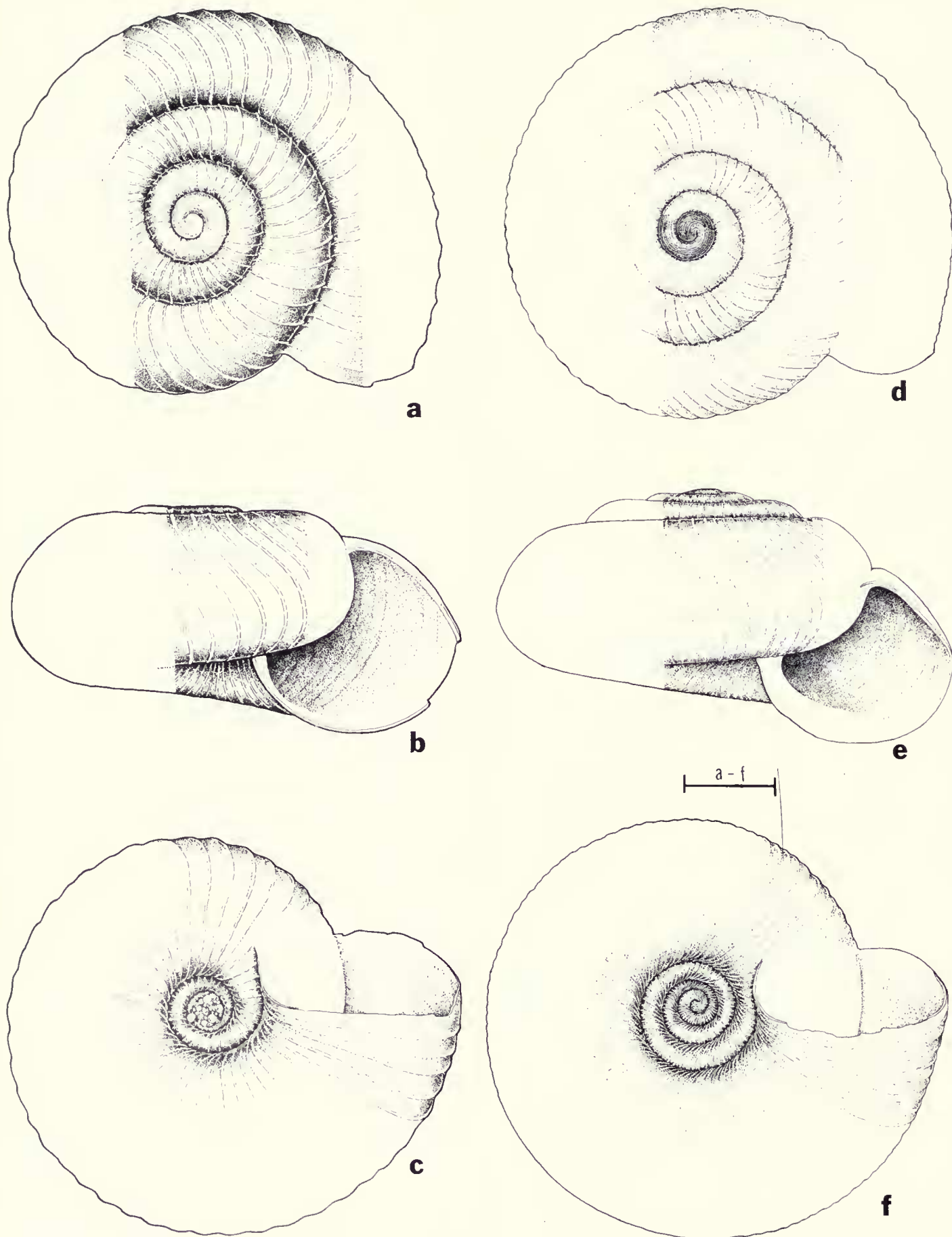


FIG. 50. a–c, *Sinployea otareae* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2335; d–f, *Sinployea tenuicostata* (Garrett). Rarotonga, Cook Islands. Paratype. BPBM 2325. Scale lines equal 1 mm. (a–c, MM; d–f, SH).



*Description*.—Shell extremely large, with 4% relatively tightly coiled whorls. Apex and early spire flat, later whorls descending gradually, body whorl descending moderately, H/D ratio 0.470. Apical whorls 1%, sculpture of 8 prominent spiral ribs with a microsculpture of radial corrugations. Postnuclear whorls with prominent, high, protractively sinuated radial ribs, 110 on the body whorl, whose interstices are 2–3 times their width. Microsculpture a lattice of radial riblets, 6–9 between each pair of major ribs, and slightly smaller, more crowded spiral riblets. Sutures deep, whorls flattened laterally above periphery and on basal margin. Color reddish yellow-brown. Umbilicus moderately open, V-shaped, regularly decoiling, contained 3.98 times in the diameter. Aperture ovate, flattened laterally above periphery and basally, inclined about 20° from the shell axis. Height of lectotype 2.34 mm., diameter 4.97 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47755.

*Range*.—Under dead wood on the banks of a stream in a single valley on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2335, ANSP.

*Material*.—Cook Islands (2 specimens, NMWC): Rarotonga (30 specimens, BPBM 167418–9, FMNH 46411, FMNH 90615).

*Remarks*.—*Mautodontha zebrina* came from the same unidentified valley (Garrett, 1881, p. 387). *Sinployea otareae* was abundant and "Living examples are uniform deep black" (Garrett, 1872, p. 229). Only minor size variation was observed (table XXIII).

***Sinployea tenuicostata*** (Garrett, 1872). Figure 50d–f.

*Pitys tenuicostata* Garrett, 1872, Am. J. Conchol., 7 (4), p. 229, pl. 19, fig. 23—rare, but widely distributed on Rarotonga, Cook Islands.

*Patula tenuicostata* (Garrett), Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 94; Garrett, 1881, J. Acad. Nat. Sci., Philadelphia, 8 (4), p. 385.

*Helix tenuicostata* (Garrett), Pfeiffer, 1876, Monog. helic. viv., 7, p. 547.

*Helix (Patula) tenuicostata* (Garrett), Tryon, 1887, Man. Conchol., (2) 3, p. 39, pl. 8, figs. 35–37.

*Endodonta (Charopa) tenuicostata* (Garrett), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Diagnosis*.—Shell very large, diameter 4.08–5.43 mm. (mean 4.70 mm.), with 3%–4% relatively loosely coiled whorls. Apex and early spire flat or barely depressed, later whorls descending slightly, H/D ratio 0.437–0.537 (mean 0.499). Apical sculpture of 9–12 (mean 10.45) prominent spiral cords. Postnuclear whorls with narrow, widely spaced, protractively sinuated radial ribs, 43–66 (mean 50.7) on the body whorl, whose interstices are 3–6 times their width. Ribs/mm. 2.87–4.23 (mean 3.46). Microsculpture of rather large and widely spaced radial riblets, 8–12 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus relatively narrow, U-shaped, regularly decoiling, contained 4.29–6.20 times (mean 5.16) in the diameter, margins rounded. Aperture strongly flattened laterally above periphery.

*Sinployea tenuicostata* (fig. 50d–f) has few and widely spaced major radial ribs, a flat spire, and relatively few and larger microradial riblets. The Samoan *S. complementaria* (fig. 56a–f) has an elevated spire, more major radials, and much finer and more numerous microradial riblets. *Sinployea otareae* (fig. 50a–c) is the same size, but has an elevated spire, many more radial ribs, and a wider umbilicus.

*Description*.—Shell very large, with 4% loosely coiled whorls. Apex and spire flat, last whorl descending slightly, H/D ratio 0.508.

Apical whorls 1%, sculpture of 11 moderately prominent spiral ribs with a faint microsculpture of radial corrugations. Postnuclear whorls with narrow, prominent, rather widely spaced, protractively sinuated radial ribs, 47 on the body whorl, whose interstices are 3–5 times their width. Microsculpture of fine, rather widely spaced radial riblets, 6–10 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deep, whorls strongly rounded above, flattened laterally above periphery and slightly on basal margin. Color light yellow-horn without darker maculations. Umbilicus narrow, U-shaped, regularly decoiling, contained 5.25 times in the diameter. Aperture subcircular, flattened laterally above periphery, inclined about 25° from the shell axis. Height of lectotype 2.11 mm., diameter 4.15 mm.

*Lectotype*.—Cook Islands: Rarotonga. Collected by Andrew Garrett. ANSP 47702.

*Range*.—Widely distributed on Rarotonga, Cook Islands.

*Paratypes*.—BPBM 2325, ANSP.

*Material*.—Rarotonga (8 specimens, Zürich, SMF 165748).

*Remarks*.—Originally described as a "somewhat rare species, having a wide range on the island, and generally found on the ground on the sides of ravines" (Garrett, 1872, p. 229), later *Sinployea tenuicostata* was termed "comparatively rare" (Garrett, 1881, p. 385). Available sets showed considerable size variation (table XXIII), which is probably magnified by the lack of clear differentiation into preadult and gerontic growth.

#### SAMOAN AND SWAINS ISLAND *Sinployea*

Except for Ofu and Olosega, every island in the Samoan group that has been collected on has yielded at least one species of *Sinployea*. Only one endodontid, *Minidonta manuaensis* Solem (1976b, p. 130), has been collected on Olosega, and no specimens of this family have been taken on Ofu. Although only two examples of *Sinployea clista* have been taken on Tutuila, comparatively little collecting has been done on that island. Aunuu Island off Tutuila has an endemic species, *S. aunuuana*, which also is recorded from Ta'u on the basis of a single very worn individual that may represent an undescribed species. *Sinployea clausa* and *S. allecta tauensis* are restricted to Ta'u in the Manu'a Group. All three Ta'u species have been found at a single station (Station 76), and *S. clausa* and *S. a. tauensis* were collected together at Stations 75, 184, 188, and 189. None of the Ta'u examples were collected alive. Scattered collections from Savai'i produced abundant material of *Sinployea allecta allecta* (Cox) from lowland localities. Much less abundant material of a more heavily ribbed form of this subspecies was collected from diverse localities and at several elevations on Upolu. At the foot of Mt. Tafua Upolu (Station 7), *S. clista* was taken together with *S. a. allecta*, whereas both *S. clista* and *S. complementaria* (Mousson) occurred at the foot of Mt. Solaua (Station 18). The latter is the dominant species on Upolu, and I suspect it is significant that *S. allecta* (Cox) and *S. complementaria* (Mousson) have not been collected at the same

stations. Swains Island has an endemic species, *Sinployea intermedia*.

No adult examples of Upolu *S. allecta allecta* were available for dissection, so the degree of difference from *S. clista* remains uncertain. The latter has a penis about 1.2 mm. long, whereas Savai'i examples of *S. allecta* have a 1.3–1.5 mm. penis with vergic papilla enlarged and stimulatory pad reduced in size. *Sinployea complementaria* is immediately differentiated by its very large penis of more than 2.0 mm. in length. Study of Upolu *S. allecta* would be desirable in order to determine the pattern of species isolation in penis structure.

Compared with the Cook and Society Island species, Samoan *Sinployea* tend to have many radial microriblets, lack secondary spiral cording (except *S. clausa* and *S. clista*), tend toward a narrowed or closed umbilicus (except *S. aunuuana*), and have a flat apex but elevated spire (table XXIV). *Sinployea aunuuana* (fig. 52a–c) has the widest umbilicus and relatively crowded major radial ribbing. Its flat spire and more

rounded body whorl ally it to the Samoan taxa. *Sinployea clista* (fig. 51a–c) and *S. clausa* (fig. 51d–f) are small species with rather widely spaced ribbing whose umbilici are closed or with only a narrow lateral crack. *Sinployea clausa* has the umbilicus open to the apex and the spire more elevated than in *S. clista* where the umbilicus is never open to the apex. Both of these have rather prominent secondary spiral cording. *Sinployea allecta* (fig. 54a–c) and *S. intermedia* (fig. 52d–f) are larger, have a more open umbilicus, at most faint traces of secondary spiral cording, and rather widely spaced major radial ribs. *Sinployea complementaria* (fig. 56a–f) is the largest known species in the genus, has an increased whorl count, very few radial ribs, and a moderately open umbilicus. *Sinployea intermedia* is the easternmost Polynesian species to lack gray pigmentation on the head and ommatophores. Since Swains Island is low and has coastal scrub rather than dense forest, restriction of this species to the ground stratum and loss of pigmentation would not be surprising.

TABLE XXIV. - RANGE OF VARIATION IN SAMOAN AND SWAINS ISLAND SINPLOYEA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO				
<u>clausa</u>	36	86.6(67–106)	11.80(9.04–14.23)	1.51(1.25–1.97)	2.41(2.11–2.93)	0.625(0.577–0.732)				
<u>clista</u>	10	98.3(74–115)	11.98(9.13–14.36)	1.50(1.28–1.84)	2.53(2.17–2.96)	0.591(0.555–0.636)				
<u>aunuuana</u>	136	112.6(92–131)	13.13(11.18–14.57)	1.40(1.25–1.71)	2.76(2.57–3.09)	0.509(0.465–0.572)				
<u>allecta allecta</u> (Cox)										
ALL	151	89.1(56–121)	9.00(5.83–11.98)	1.77(1.51–2.04)	3.13(2.63–3.62)	0.571(0.511–0.622)				
Savaii	86	75.9(56–89)	7.84(5.85–8.97)	1.75(1.51–1.94)	3.07(2.65–3.36)	0.576(0.558–0.598)				
Upolu	65	99.3(84–121)	9.90(8.48–11.98)	1.79(1.51–2.04)	3.17(2.63–3.62)	0.567(0.511–0.622)				
<u>allecta tauensis</u>	26	79.8(61–101)	8.31(6.20–10.51)	1.73(1.61–1.97)	3.00(2.70–3.39)	0.577(0.542–0.616)				
<u>intermedia</u>	46	82.1(63–96)	7.66(5.75–9.16)	2.03(1.82–2.19)	3.49(3.21–3.81)	0.581(0.534–0.616)				
<u>complementaria</u> (Mousson)	126	69.1(52–95)	4.50(3.11–5.79)	2.55(2.11–3.32)	4.92(4.31–5.92)	0.517(0.458–0.648)				
	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW			
<u>claus.</u>	3 7/8–(3 1/2–4 3/8)	0.11(0.07–0.20)	23.1(13.7–39)	9.40(8–10)	0.19(0.16–0.23)	0.90(0.82–0.92)	0.215(0.200–0.233)			
<u>clist.</u>	3 3/4+(3 1/2–4 1/4)	LESS THAN 0.13	CLOSED OR NARROW CRACK	9.17(8–11)	0.07(0.03–0.13)	0.98(0.86–1.12)	0.089(0.033–0.176)			
<u>aunuu.</u>	4 1/8–(4–4 1/2)	0.75(0.66–0.95)	3.69(3.24–4.05)	9.50(8–12)	0.13(0.07–0.26)	0.89(0.82–0.92)	0.125(0.074–0.286)			
<u>a.all.</u>										
ALL	4 1/8(3 5/8–4 1/2)	0.41(0.26–0.59)	7.85(5.93–9.80)	8.60(7–10)	0.14(0.07–0.23)	1.11(0.99–1.22)	0.123(0.056–0.250)			
Sav.	4+(3 5/8–4 3/8)	0.39(0.33–0.43)	7.89(6.85–9.20)	8.50(8–9)	0.16(0.12–0.21)	1.09(0.99–1.15)	0.143(0.103–0.191)			
Upo.	4 1/8+(3 7/8–4 1/2)	0.42(0.26–0.59)	7.82(5.93–9.80)	8.70(7–10)	0.13(0.07–0.23)	1.12(1.02–1.22)	0.117(0.056–0.250)			
<u>a.tau.</u>	4–(3 3/4–4 1/8)	0.46(0.33–0.69)	6.80(4.72–9.55)	UNKNOWN	0.19(0.18–0.20)	1.09(1.05–1.12)	0.172(0.162–0.188)			
<u>inter.</u>	4 3/8+(4 1/4–4 3/4)	0.64(0.53–0.79)	5.43(4.59–6.12)	10.57(9–13)	0.23(0.13–0.35)	1.12(1.02–1.25)	0.209(0.125–0.309)			
<u>compl.</u>	4 5/8+(4 3/8–5 1/4)	0.99(0.76–1.22)	4.99(4.18–6.08)	10.08(8–13)	0.22(0.07–0.46)	1.55(1.35–1.81)	0.140(0.039–0.275)			



KEY TO SAMOAN AND SWAINS ISLAND *Sinployea*

1. Umbilicus closed or D/U ratio averaging more than 20 .....2  
Umbilicus open, D/U ratio averaging much less than 10.....3
2. Spire protrusion about  $\frac{1}{2}$  body whorl width; umbilicus with apex visible.....*Sinployea clausa*, new species  
Spire protrusion averaging less than 0.10; umbilicus closed or at most a lateral crack.....*Sinployea clista*, new species
3. Diameter less than 4.00 mm.; ribs/mm. averaging more than 6.00.....4  
Diameter more than 4.00 mm.; ribs/mm. averaging less than 5.00.....*Sinployea complementaria* (Mousson, 1865)
4. D/U ratio averaging more than 5.00; H/D ratio averaging more than 0.550.....5  
D/U ratio averaging about 3.75; H/D ratio about 0.510 .....  
*Sinployea aunuuana*, new species
5. Mean diameter about 3.0–3.2 mm.; mean D/U ratio more than 6.50.....6  
Mean diameter about 3.5 mm.; mean D/U ratio about 5.50; Swains Island.....*Sinployea intermedia*, new species
6. Spire more protruded; umbilicus slightly wider; Ta'u, Manu'a Group.....*Sinployea allecta tauensis*, new subspecies  
Spire less protruded; umbilicus slightly narrower; Upolu and Savai'i.....*Sinployea allecta allecta* (Cox, 1870)

***Sinployea clausa*, new species. Figure 51d–f.**

**Diagnosis.**—Shell small, diameter 2.11–2.93 mm. (mean 2.41 mm.), with  $3\frac{1}{2}$ –4% normally coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending much more rapidly, spire protrusion more than  $\frac{1}{2}$  body whorl width, H/D ratio 0.577–0.732 (mean 0.625). Apical sculpture of 8–10 (mean 9.40) fine spiral cords. Postnuclear whorls with narrow, rounded, protractive, rather inconspicuous radial ribs, 67–106 (mean 86.6) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 9.04–14.2 (mean 11.80). Microsculpture of extremely fine radial riblets, 5–10 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Secondary sculpture of fine, rather widely spaced spiral cords visible over entire shell surface. Umbilicus very narrow, open to apex, about  $\frac{1}{3}$  constricted by basal lip, contained 13.7–39 times (mean 23.1) in the diameter, margins rounded. Whorl profile almost circular, only flattened slightly on upper palatal wall, basal margin rounded, aperture inclined about 5° from shell axis.

*Sinployea clista* (compare fig. 51a–c) is very closely related, differing primarily in its lower spire and generally imperforate or at most very narrowly open umbilicus. Other Samoan species have wider umbilici. Extralimital species with narrow umbilici, such as *Ba humbugi* (fig. 74a–c) and *Sinployea adposita* (fig. 69d–f) from Fiji, have vastly different shapes and sculpture.

**Description.**—Shell small, with 4 tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending much more rapidly, H/D ratio 0.613. Embryonic whorls  $1\frac{1}{2}$ , sculpture partly eroded, remnants of about 9 spiral cords. Remaining whorls with moderately prominent, rounded, protractive radial ribs, 89 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of very fine radial riblets, 5–12 between each pair of major ribs, even finer spiral riblets and larger, relatively widely spaced, secondary spiral cords. Sutures deeply impressed, whorls strongly rounded above with only slight lateral flattening. Umbilicus barely perforate, partially constricted by basal lip, contained 15 times in the diameter. Color a uniform, very light yellow-brown. Aperture circular with slightly expanded baso-columellar margin, slightly flattened laterally above periphery, inclined about 5° from the shell axis. Height of holotype 1.51 mm., diameter 2.47 mm.

**Holotype.**—Samoa: Ta'u, Station 188, Faleasao, 700 ft. inland, at 12 ft. elevation. Collected by Wray Harris on September 24, 1937. BPBM 187736.

**Range.**—Ta'u, Manu'a Group, American Samoa.

**Paratypes.**—Ta'u: Siufaga (Stations 16, 76, 138, 184, 185, 186, 211) at 350–600 ft. inland at 5–500 ft. elevation (19 specimens, BPBM 171136, BPBM 173784, ex BPBM 171073, ex BPBM 182410, ex BPBM 187653, BPBM 186682, BPBM 187625, BPBM 187658, BPBM 187705, BPBM 188085); Tavalagi,  $\frac{1}{2}$  mile inland (Station 75) at 500 ft. elevation above Faleasao cliffs (3 specimens, BPBM 171065, ex BPBM 171106, ex BPBM 182095); Faleasao, 600–700 ft. inland (Stations 185, 188–190) at 12 ft. elevations (11 specimens, BPBM 187665, BPBM 187728, BPBM 187736, BPBM 187774, ex BPBM 187753, ex BPBM 187781, BPBM 187982, BPBM 188277); Amouli,  $\frac{1}{2}$  mile inland (Station 80) at 500 ft. elevation (1 specimen, BPBM 182150); Palapala,  $\frac{1}{2}$  mile inland (Station 201) at 600 ft. elevation (1 specimen, BPBM 187919).

**Remarks.**—The only available specimens were dead shells taken from sweepings mixed in coral rubble. A high percentage of the shells had bits of coral stone and sand cemented to the shell surface, and many were quite worn. Specimens from Faleasao did not differ significantly from those taken at Siufaga (table XXV).

The name *clausa*, from the Latin meaning closed, is perhaps slightly misleading, because the umbilicus is always minutely perforate, but the name was chosen to emphasize its close relationship to *Sinployea clista* from Upolu and Tutuila.

In combining a higher spire and wider umbilicus than is found in *S. clista*, *S. clausa* parallels (fig. 51a–f) the divergence seen between the subspecies of *S. allecta* (fig. 54a–e). Only the proportionately greater size of the morphologic gap between *S. clista* and *S. clausa* accounts for the arbitrary consideration of them as species rather than subspecies.

***Sinployea clista*, new species. Figures 51a–c, 53d–e.**

**Diagnosis.**—Shell small, diameter 2.17–2.96 mm. (mean 2.53 mm.), with  $3\frac{1}{2}$ –4% normally coiled whorls. Apex and spire flat to slightly and evenly elevated, body whorl descending much more rapidly, spire protrusion less than  $\frac{1}{10}$  body whorl width, H/D ratio 0.555–0.636 (mean 0.591). Apical sculpture of 8–11 (mean 9.17) narrow spiral cords. Postnuclear whorls with low, rounded, protractively constricted radial ribs, 74–115 (mean 98.3) on the body whorl, whose interstices are about 3–4 times their width except becoming crowded and indistinct on end of body whorl. Ribs/mm. 9.13–14.36 (mean 11.98). Microsculpture of very fine radial riblets, 5–12 between each pair of major ribs, crossed by slightly finer spiral riblets, relatively crowded and inconspicuous secondary spiral cording visible on most of shell surface. Umbilicus either closed (50%) or with a narrow lateral opening that prevents seeing the apex, contained more than 20 times in the diameter. Whorls strongly rounded on all margins, very slightly flattened laterally above periphery, aperture inclined about 15° from shell axis.

*Sinployea clausa* (fig. 51d–f) has the umbilicus narrowly open and the spire distinctly more elevated. Other minor differences are discussed below. *Ba humbugi* (fig. 74a–c) from Fiji has a much more elevated spire (mean H/D ratio 0.817) and very few and widely spaced major radial ribs. All other *Sinployea* are at least narrowly umbilicated.

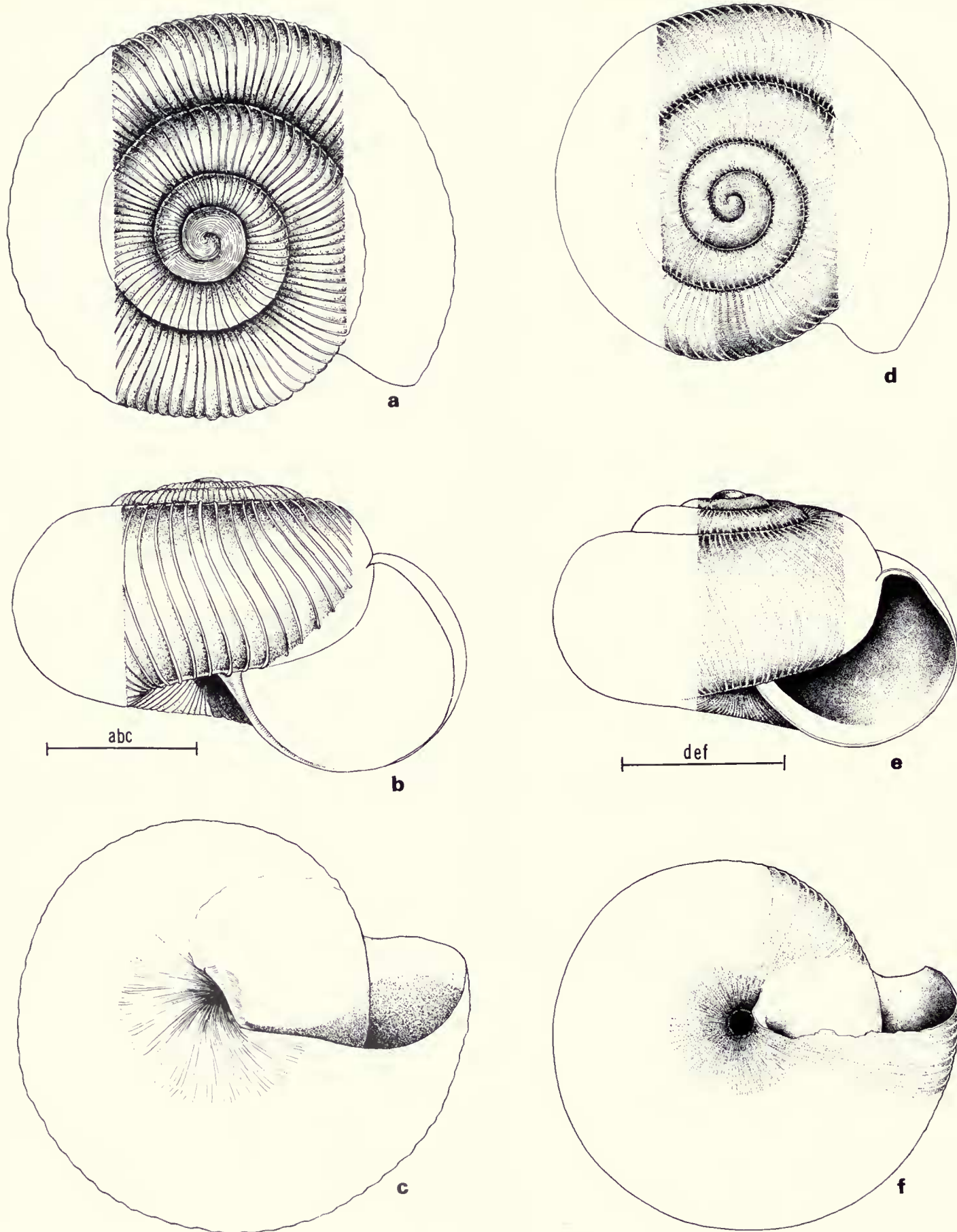


FIG. 51. **a-c**, *Sinployea clista*, new species. Olomoana, Tutuila, Samoa. Holotype. BPBM 84372; **d-f**, *Sinployea clausa*, new species. Station 188, Faleasao, Ta'u, Samoa. Holotype. BPBM 187736. Scale lines equal 1 mm. (**a-c**, SG; **d-f**, MM).



TABLE XXV. - LOCAL VARIATION IN SAMOAN SINPLOYEA, I.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>clausa</u>					
Faleasao	10	88.1±15.88 (75-101)	1.47±0.063 (1.22-1.81)	2.38±0.080 (2.07-2.93)	0.615±0.0006 (0.577-0.666)
Siufaga	11	85.6±4.33 (67-106)	1.54±0.050 (1.38-1.97)	2.42±0.050 (2.20-2.70)	0.637±0.0122 (0.584-0.732)
<u>clista</u>					
Tutuila BPBM 84372	2	89.0±6.02 (83-95)	1.84	2.93±0.033 (2.89-2.96)	0.629±0.0070 (0.622-0.636)
Upolu BPBM 185879, BPBM 186642	3	74	1.29±0.011 (1.28-1.32)	2.23±0.039 (2.17-2.30)	0.582±0.0055 (0.572-0.591)
FMNH 153177, DMW MF3992	3	112.7±2.34 (108-115)	1.48±0.050 (1.41-1.58)	2.57±0.025 (2.53-2.63)	0.575±0.0130 (0.555-0.600)
<u>aunuuanā</u>					
BPBM 83242	25	-----	1.41±0.018 (1.26-1.72)	2.76±0.024 (2.58-3.11)	0.508±0.0050 (0.465-0.556)
<u>allecta allecta</u>					
Upolu AMS, BPBM	18	97.1±5.10 (78-121)	1.76±0.043 (1.39-2.02)	3.09±0.064 (2.52-3.41)	0.567±0.0073 (0.511-0.622)
Zurich	13	101.8±3.72 (84-121)	1.84±0.020 (1.71-2.01)	3.26±0.044 (3.03-3.55)	0.566±0.0045 (0.543-0.598)
Savaii Sta. 38 FMNH 153371	6	73.4±1.86 (69-80)	1.75±0.064 (1.51-1.94)	3.04±0.096 (2.66-3.36)	0.576±0.0064 (0.558-0.598)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>clausa</u>					
Fale.	3 3/4+(3 1/2-4 1/8)		0.12±0.011 (0.07-0.20)	22.4±2.19 (14.8-39)	9.25±0.48 (8-10)
Siuf.	3 7/8+(3 1/2-4 3/8)		0.12±0.012 (0.07-0.20)	22.7±2.07 (13.6-35)	-----
<u>clista</u>					
Tutu.	4 1/4		0.13	22.5	10.0±1.0 (9-11)
Upolu BPBM	3 5/8(3 1/2-3 3/4)		0.08±0.011 (0.07-0.10)	29.9±3.3 (23.3-33.5)	9
FMNH	3 5/8+(3 5/8-3 3/4)		-----	-----	8.5±0.50 (8-9)
<u>aunuuanā</u>					
BPBM	4 1/8-(4-4 1/2)		0.74±0.014 (0.66-0.95)	3.69±0.044 (3.24-4.05)	9.00±0.55 (8-11)
<u>a.allecta</u>					
Upolu AMS	4 1/8(3 7/8-4 3/8)		0.39±0.015 (0.26-0.49)	8.05±0.250 (5.93-9.70)	8.33±0.67 (7-9)
Zurich	4 1/8+(4-4 3/8)		0.43±0.020 (0.33-0.53)	7.74±0.316 (6.19-9.80)	8.83±0.48 (7-10)
Savaii Sta. 38	4-(3 5/8-4 1/4)		0.39±0.020 (0.33-0.43)	7.89±0.356 (6.85-9.20)	8.50 (8-9)

*Description*.—Shell small, with  $4\frac{1}{4}$  normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending much more rapidly, H/D ratio 0.622. Embryonic whorls  $1\frac{1}{2}$ , sculpture of 11 narrow spiral cords with an intrusion of vague radial corrugations on last quarter whorl. Postnuclear whorls with low, rounded, protractively sinuated radial ribs, 93 on the body whorl, whose interstices are 2–4 times their width, becoming irregular and more crowded on gerontic portions of body whorl. Microsculpture of fine radial riblets, 5–10 between each pair of major ribs, exceedingly fine spiral riblets, and inconspicuous secondary spiral cords. Sutures deep, whorls flatly rounded above periphery with broadly rounded basal margin, sloping to narrow umbilical chink. Umbilicus closed by expansion of inner portion of body whorl and reflection of umbilical lip. Color light yellow-brown with reddish markings. Aperture circular with slightly less sharply rounded suprapерipheral outer margin, inclined about  $15^\circ$  from shell axis. Height of holotype 1.84 mm., diameter 2.96 mm.

*Holotype*.—Samoa: Tutuila, Olomoana. Collected under stones and on dead leaves by members of the Samoan Expedition on March 17, 1926. BPBM 84372.

*Range*.—Tutuila, American Samoa, and Upolu, Western Samoa.

*Paratypes*.—Tutuila: Olomoana, under stones and dead leaves (1 specimen, BPBM 84372). Upolu: Mt. Vaea (Station 147) at 850 ft. elevation (3 specimens, BPBM 185879); Tatapao-Lake Lanuto'o trail at 1,250 ft. elevation (1 specimen, BPBM 186642); foot of south-east peak, Mt. Tafua Upolu (Station 7) at 1,200 ft. elevation (1 specimen, FMNH 153081); foot of Mt. Solaua (Station 18) at 600–800 ft. elevation (2 specimens, FMNH 153177); Tanumalala at 800 ft. elevation (1 specimen, DMW MF 3992, collected by R. A. Cumber on May 15, 1954).

*Remarks*.—Besides the obvious differences in spire protrusion and umbilical closure, *Sinployea clista* differs from *S. clausa* in having the aperture more strongly inclined and the major ribbing protractively sinuated rather than being just slightly inclined. The latter also has the secondary spiral cording more prominent and more widely spaced.

*Sinployea clista* is sparsely distributed on both Upolu and Tutuila. Although there are obvious size, shape, and ribbing differences (tables XXIV–XXV), so little material is available that I give no systematic recognition to these variations. Despite intensive efforts after field recognition, no additional examples could be located at the Mt. Tafua Upolu and Mt. Solaua stations.

The name *clista* is taken from the Greek for closed and refers to the unusual umbilicus.

*Description of soft parts*.—Pallial region (fig. 53e) about 3.5 mm. long, rectal kidney lobe 1.7 mm. long, much longer than pericardial arm. Space between ureter arms wider than in most Polynesian species.

Genitalia (fig. 53d) fragmentary, observed portions without unusual features. Penis about 1.2 mm. long.

(Based on BPBM 84372, 1 partial example.)

***Sinployea aunuuana*, new species.** Figures 52a–c, 53a–c.

*Diagnosis*.—Shell slightly smaller than average, diameter 2.57–3.09 mm. (mean 2.76 mm.), with  $4\frac{1}{2}$  normally coiled whorls. Apex and early spire flat or slightly protruding, lower spire whorls

descending slightly, body whorl descending rapidly, spire protrusion about  $\frac{1}{4}$  body whorl width, H/D ratio 0.465–0.572 (mean 0.509). Apical sculpture of 8–12 (mean 9.50) narrow spiral cords. Postnuclear sculpture of very fine, narrow, rather crowded, slightly protractively sinuated radial ribs, 92–131 (mean 112.6) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 11.18–14.57 (mean 13.13). Microsculpture of very fine radial riblets, 5–9 between each pair of major ribs, crossed by very fine and crowded spiral riblets, with an indistinct development of secondary spiral cording occasionally visible. Umbilicus broadly open, V-shaped, regularly decoiling, contained 3.24–4.05 times (mean 3.69) in the diameter, margins rounded. Whorl contours slightly less compressed than average, aperture inclined about  $10^\circ$  from shell axis.

The generally flat apex and early spire of *Sinployea aunuuana* (fig. 52a–c) combine with the wide umbilicus and crowded radial ribbing to easily separate it from the other Polynesian species. Of similar-sized species, *S. neglecta* (fig. 41d–f) from Huahine has a much more elevated spire, proportionately narrower umbilicus, and about 12.5 apical cords; *S. atiensis* (fig. 44d–f) has a higher spire and narrower umbilicus with broader and more widely spaced ribs. *Sinployea kusaieana* (fig. 63a–c) has a narrower body whorl, fewer whorls, and a proportionately smaller apex.

*Description*.—Shell slightly smaller than average, with  $4\frac{1}{4}$  tightly coiled whorls. Apex and early spire flat, body whorl descending rapidly, spire protrusion about  $\frac{1}{10}$  of body whorl width, H/D ratio 0.524. Embryonic whorls  $1\frac{1}{2}$ , sculpture of 12 moderately prominent spiral ribs. Postnuclear whorls with somewhat irregularly spaced, high, rounded radial ribs, 123 on the body whorl, whose interstices are usually about twice their width. Microsculpture of very fine radial riblets, 3–6 between each pair of major ribs, crossed by barely visible, spiral riblets that are very crowded. Occasional traces of weak spiral cording. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above periphery and slightly on basal margin. Umbilicus broadly V-shaped, widely open, regularly decoiling, contained 3.82 times in the diameter. Color uniform light reddish brown. Aperture circular, strongly flattened laterally above periphery, inclined about  $10^\circ$  from the shell axis. Height of holotype 1.45 mm., diameter 2.77 mm.

*Holotype*.—Samoa: Aunuu Island (off Tutuila), Station 14, 500 yd. from shore at 200 ft. elevation. Collected by T. T. Dranga on February 4, 1926. BPBM 83256.

*Range*.—Aunuu Island off Tutuila and probably Ta'u, Manu'a Group, American Samoa.

*Paratypes*.—Aunuu: 10 yd. east of lighthouse, 200 yd. inland at 250 ft. elevation (134 specimens, BPBM 83242). Ta'u: Siufaga swamp, 400 ft. inland (Station 76) at 7 ft. elevation (1 specimen, ex BPBM 182444).

*Remarks*.—Although the size and umbilical shape of *Sinployea aunuuana* (fig. 52a–c) is more similar to the Cook and Society Island species, the very fine radial riblets, wide body whorl, flat spire, and round whorl contours relate it to the other Samoan species. *Sinployea allecta* (fig. 54a–e) is most similar, but differs in its much narrower umbilicus, more elevated shape (table XXIV), and absence of secondary spiral cording. They agree in their spire shape and relative protrusion.

A single dead, very worn specimen from Ta'u is referred here with some hesitation. In size and propor-



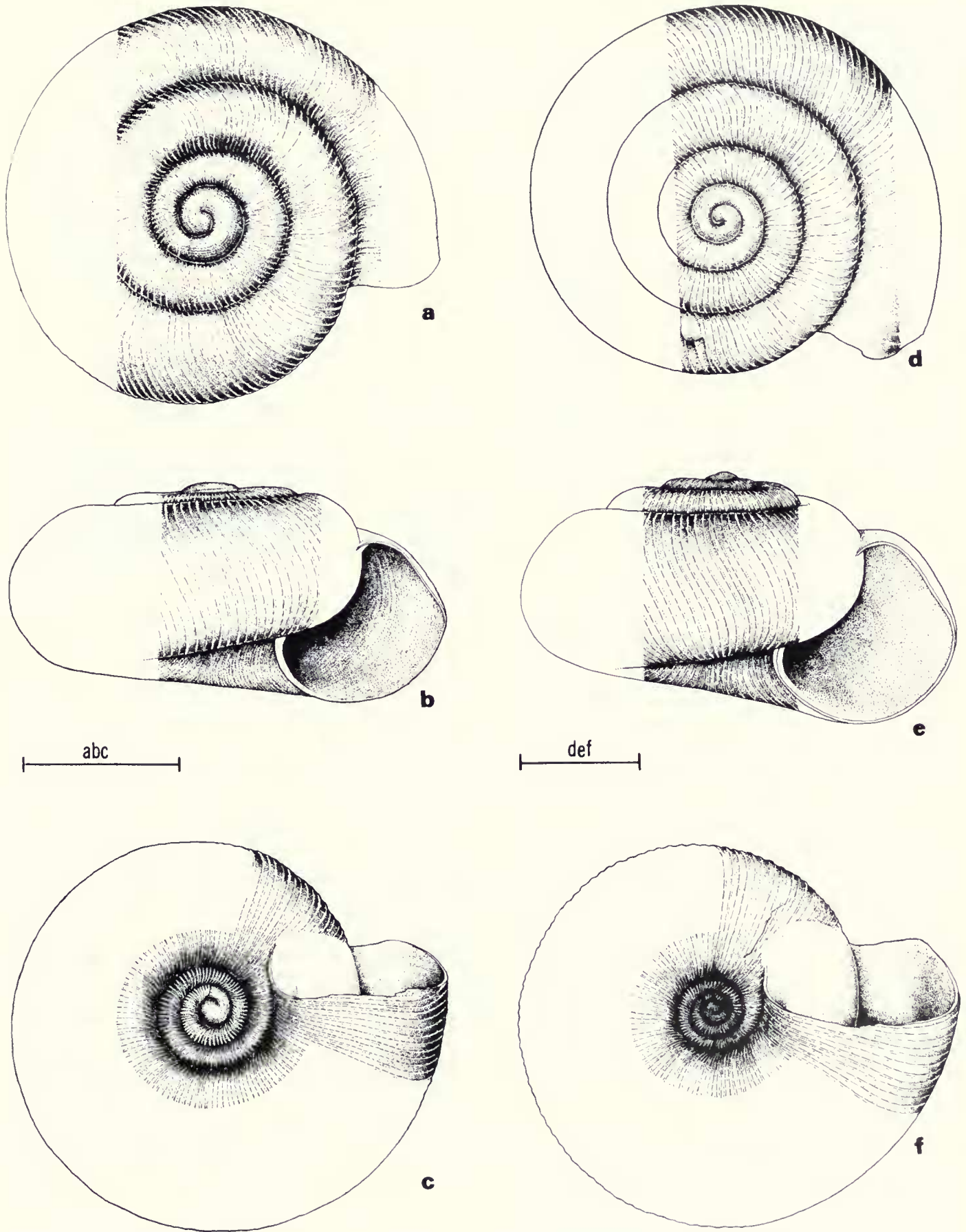


FIG. 52. **a-c**, *Sinployea aunuuana*, new species. Station 14, Aunuu Island, Tutuila, Samoa. Holotype. BPBM 83256; **d-f**, *Sinployea intermedia*, new species. 200 yd. inland, west side Swains Island. Holotype. BPBM 186666. Scale lines equal 1 mm. (MM).

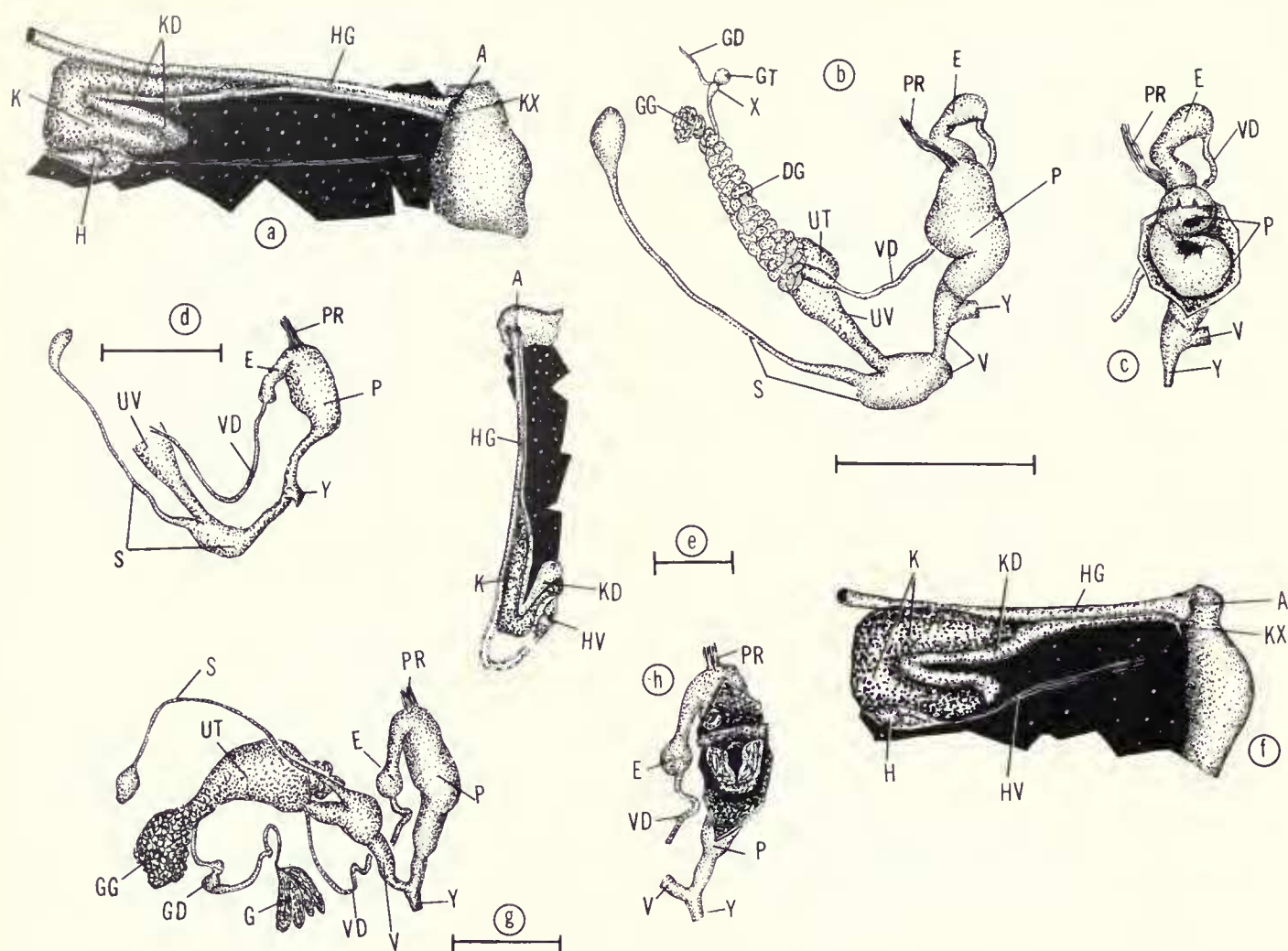


FIG. 53. Anatomy of *Sinployea aunuuana*, *S. clista*, and *S. intermedia* from Samoa and Swains Island: a–c, *Sinployea aunuuana*, new species. Station 14, Aunuu, Tutuila, Samoa. BPBM 83256. a, pallial region. b, genitalia. c, interior of penis with muscular collar not slit open; d–e, *Sinployea clista*, new species. Olomoana, Tutuila, Samoa. BPBM 84372. d, terminal genitalia. e, pallial region; f–h, *Sinployea intermedia*, new species. West side of Swains Island. BPBM 186666. f, pallial region. g, genitalia. h, penis interior. Scale lines equal 1 mm. (MO).

tions it falls within the midrange of variation, height 1.35 mm., diameter 2.63 mm., H/D ratio 0.512, whorls  $4\frac{1}{8}$ , D/U ratio 3.64. The spire is slightly more elevated than normal, and this may be misidentified. If so, it represents an undescribed species.

*Description of soft parts.*—Pallial region (fig. 53a) about 3.3 mm. long, rectal kidney lobe much longer than pericardial, about 1.35 mm. long.

Genitalia (fig. 53b) without unusual features. Penis length about 1.0 mm., internally (fig. 53c) penis with verge, collar, and stimulatory pad. Latter drawing with collar shown intact, verge not visible.

(Based on BPBM 83256, 1 example.)

### *Sinployea allecta* (Cox, 1870).

Material from Ta'u, Upolu, and Savai'i is sufficiently similar in size, shape, and sculpture (table XXV) to be considered conspecific. The Swains Island *S. intermedia* (fig. 52d–f) is conspicuously larger, has a wider umbilicus, and averages two more apical spiral cords. *Sinployea aunuuana* (fig. 52a–c) has the umbilicus much more widely open (mean D/U ratio 3.69 as

compared to more than 6.5 in *allecta*) and possesses relatively conspicuous secondary spiral cording. *Sinployea complementaria* (fig. 56a–f) is much, much larger (table XXIV) and has more widely spaced radial ribs.

Taxonomic treatment of the *S. allecta* material is partly arbitrary. The populations on Ta'u are subspecifically distinct, differing significantly in having both a higher spire and a wider umbilicus. Usually a lower spire means a wider umbilicus, and a higher spire accompanies a narrower umbilicus. Hence, the shifts in the Ta'u populations are separate rather than being linked. Subspecific status has been chosen because the similarities are many. Populations on Savai'i and Upolu show no significant differences in size or shape, but do have markedly distinctive rib counts and spacing (table XXV). The Upolu material comes from the 1860–1870 period, whereas the Savai'i material was collected in 1965. As discussed below, only subadult *S. allecta* were taken on Upolu in 1965. The significance of this sculpture variation remains uncertain. In treat-



ing the Savai'i and Upolu populations as belonging to one subspecies, I am deferring judgment as to their exact relationship. New collections of adults from Upolu are needed to settle this problem.

***Sinployea allecta allecta*** (Cox, 1870). Figures 54a–c, 55a–e.

*Helix allecta* Cox, 1870, Proc. Zool. Soc. London, 1870, p. 81—found on the mountains under decayed wood, Upolu, Samoa; Pfeiffer, 1876, Monog. helic. viv., 7, p. 162.

*Charopa allecta* (Cox), Tryon, 1886, Man. Conchol., (2) 2, p. 210—name only.

*Patula allecta* (Cox), Garrett, 1887, Proc. Acad. Nat. Sci., Philadelphia, 1887, p. 130.

**Diagnosis.**—Shell larger than average, diameter 2.63–3.62 mm. (mean 3.13 mm.), with 3%–4½ rather tightly coiled whorls. Apex and early spire usually flat, sometimes slightly and evenly elevated, lower spire descending slightly, body whorl descending moderately, spire protrusion about ¼ body whorl width, H/D ratio 0.511–0.622 (mean 0.571). Apical sculpture of 7–10 (mean 8.60) rather fine spiral cords. Postnuclear whorls with narrow, rounded, rather prominent, and protractively sinuated radial ribs that are variable in number and spacing, 56–121 (mean 89.1) on the body whorl, whose interstices are 2–5 times their width. Ribs/mm. 5.83–11.98 (mean 9.00). Microsculpture of exceedingly fine radial riblets, 4–12 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. No secondary spiral cording visible at 96× magnification. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, slightly constricted by columellar lip expansion, contained 5.93–9.80 times (mean 7.85) in the diameter, margins rounded. Whorls almost evenly rounded on outer margins, slightly flattened laterally above periphery, aperture inclined about 15° from shell axis.

The narrower umbilicus and lower spire protrusion readily separate *Sinployea allecta allecta* (fig. 54a–c) from *S. a. tauensis* (fig. 54d–f). *Sinployea intermedia* (fig. 52d–f) is larger and has a higher spire and much wider umbilicus. Other Samoan species differ radically in size and umbilical proportions. Of extralimital species with narrow umbilici, the Lau Archipelago *S. angularis* (fig. 64d–f) and *S. recurva* (fig. 64a–c) both have reduced radial ribbing; the Tahitian *S. montana* (fig. 41a–c) is much smaller.

**Description.**—Shell smaller than average with 3% loosely coiled whorls. Apex slightly protruding, spire flat, last whorl descending a little, H/D ratio 0.554. Body whorl quite obese, sutures moderately deeply impressed, whorls strongly rounded above and on outer margins. Embryonic whorls 1%, sculpture of 9 relatively inconspicuous spiral ribs. Postnuclear whorls with moderately prominent, rounded, closely spaced, protractively sinuated radial ribs, 86 on the body whorl, whose interstices are usually slightly less than twice their width. Microsculpture of 4–8 very fine radial riblets between each pair of major ribs, and even finer and more crowded spiral riblets. Body whorl evenly rounded on outer margin with slightly protruded basal lip coming to the evenly rounded umbilical margin. Umbilicus partially constricted by inward expansion of columellar lip, narrowly U-shaped, regularly decoiling, contained 5.93 times in the diameter. Color yellowish white with relatively numerous reddish flammulations. Aperture circular with protruding basal margin, inclined about 15° from shell axis. Height of lectotype 1.53 mm., diameter 2.73 mm.

**Lectotype.**—Samoa: Upolu. Collected on the mountains under decayed wood. AMS C.63457.

**Range.**—Upolu and Savai'i, Western Samoa.

**Paratypes.**—AMS C.63458.

**Material.**—Upolu (60 specimens, BPBM 106246,

BPBM 115349, BPBM 167430, AMS C.34756, AMS C.63457-8, Zurich, FMNH 117267, FMNH 160001, SMF 165706, NMWC): Togitogiga forest area (Station 10) at 50 ft. elevation (1 specimen, FMNH 153062); foot of southeast peak (Station 7), Mt. Tafua Upolu at 1,200 ft. elevation (3 specimens, FMNH 153082); gully to foot of Mt. Siga'ele (Station 23) at 2,300 ft. elevation (1 specimen, FMNH 153426).

Savai'i: heavy forest about 5 miles (Station 30) northwest of Vailoa at 600 ft. elevation in heavy forest (20 specimens, FMNH 153039); about ½ mile inland, 5 miles east of Vailoa (Station 38) on road to Salelologa wharf in open bush (66 specimens, FMNH 153371, FMNH 153091).

**Remarks.**—The type specimens are all subadult, and Cox's whorl count of 4½–5 is in error. In older collections, specimens of this species are usually labeled as *S. complementaria*. Numerous specimens were collected by Graeffe in the early 1870s and are rather widely distributed in museum collections. This was after Mousson had published on Samoan material. Hence, they were not mentioned in the previous literature.

Although the material in historical collections and the specimens obtained by Solem and Price in 1965 agree almost exactly in dimensions and shape (table XXV), there is a marked dichotomy in ribbing. The specimens collected by Cox and Graeffe in the 1860s and 1870s on Upolu have a mean of 99.3 ribs on the body whorl and 9.90 ribs/mm. Those from Savai'i (tables XXIV–XXV) average only 75.9 ribs on the body whorl and 7.84 ribs/mm. Unfortunately, only subadult material was obtained on Upolu in 1965. The specimen from Togitogiga (Station 10) has the typical Upolu ribbing, but those from Mt. Tafua Upolu (Station 7) and near Mt. Siga'ele (Station 23) have the more widely spaced ribbing found in the Savai'i examples.

**Description of the soft parts.**—Foot and tail longer than shell diameter, bluntly rounded anteriorly, slightly tapering posteriorly. Sole undivided, pedal grooves prominent, suprapedal larger; no caudal horn or middorsal groove present. Head projecting slightly in front of foot. Ommatophores typical. Gonopore in normal position.

Body color yellow-white, with a grayish suffusion on neck, head, and back of tail.

Mantle collar (fig. 55d) without glandular extension onto pallial roof, edge swollen and providing a flap to narrow pneumostome. Anus (A) and external ureteric pore (KX) typical.

Pallial region extending ¾ whorl apically. Lung roof clear, without granulations. Kidney (K) with lobes subequal, rectal lobe 1.45 mm. long, clearly overlapping hindgut. Base slightly indented, inner side dished by organs above pallial cavity. Ureter (KD) reflexed with very little roof space between arms (fig. 55a–b), narrow, widening slightly along hindgut. Heart (H) more than half length of kidney, angled slightly from hindgut. Principal pulmonary vein (HV) simple, unbranched, angling toward pneumostome. Hindgut (HG) arising just above kidney, not tapering.

Ovotestis with one or two clumps of palmately clavate acini lying parallel to whorl sides. Hermaphroditic duct (fig. 55c, GD) narrow at first, expanded and iridescent, sharply reflexed and narrowed at apex of albumen gland, following surface of gland to base of talon head, entering latter basally. Albumen gland (GG) elongately ovate, surface indented by intestinal loops and spermathecal head. Talon (GT) with ovately globular, iridescent head partly buried in albumen

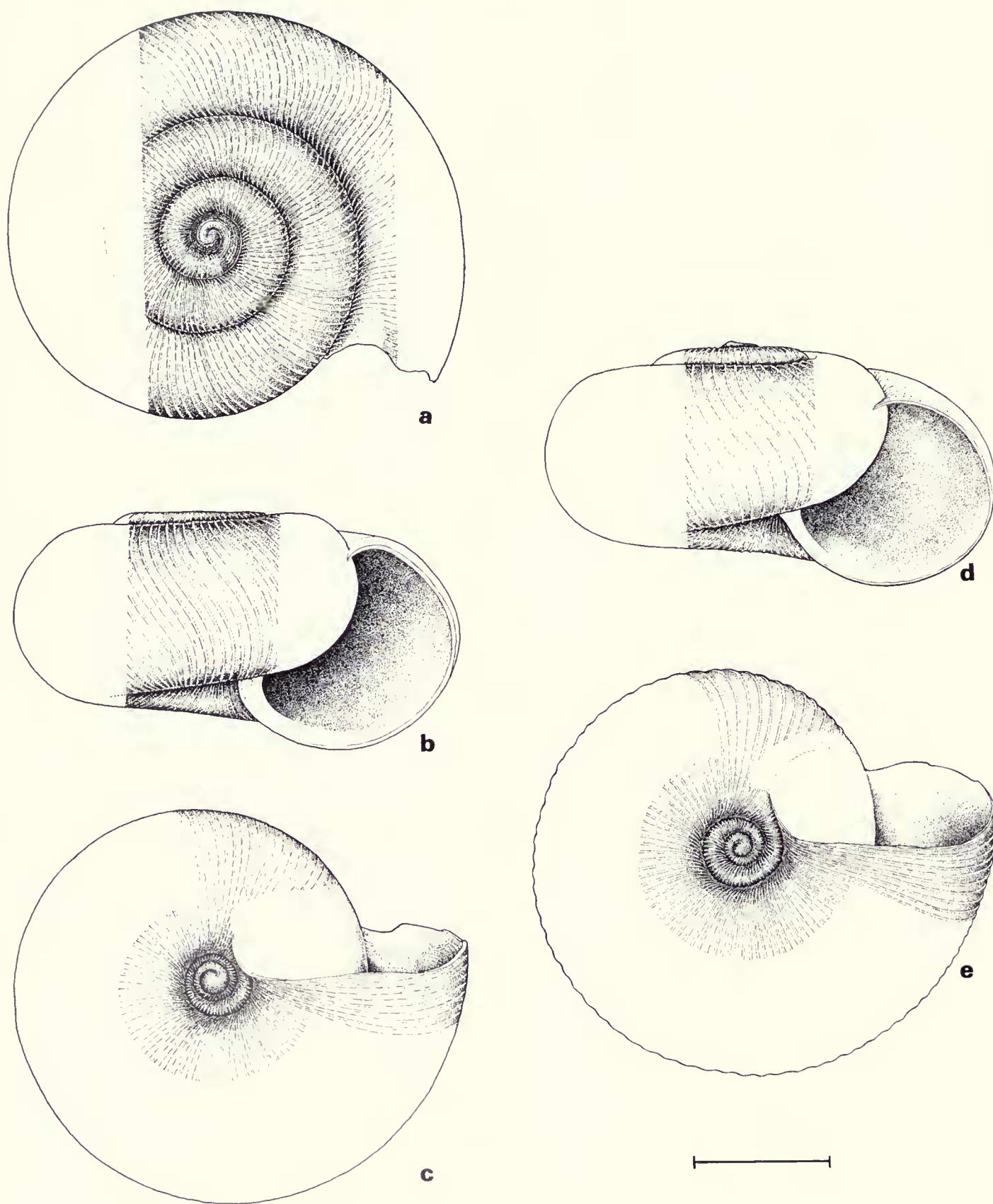


FIG. 54. a-c, *Sinployea allecta allecta* (Cox), Upolu, Samoa. BPBM 167430; d-e, *Sinployea allecta tauensis*, new subspecies. Station 188, Faleasao, Ta'u, Samoa. Holotype. BPBM 187753. Scale line equals 1 mm. (MM).



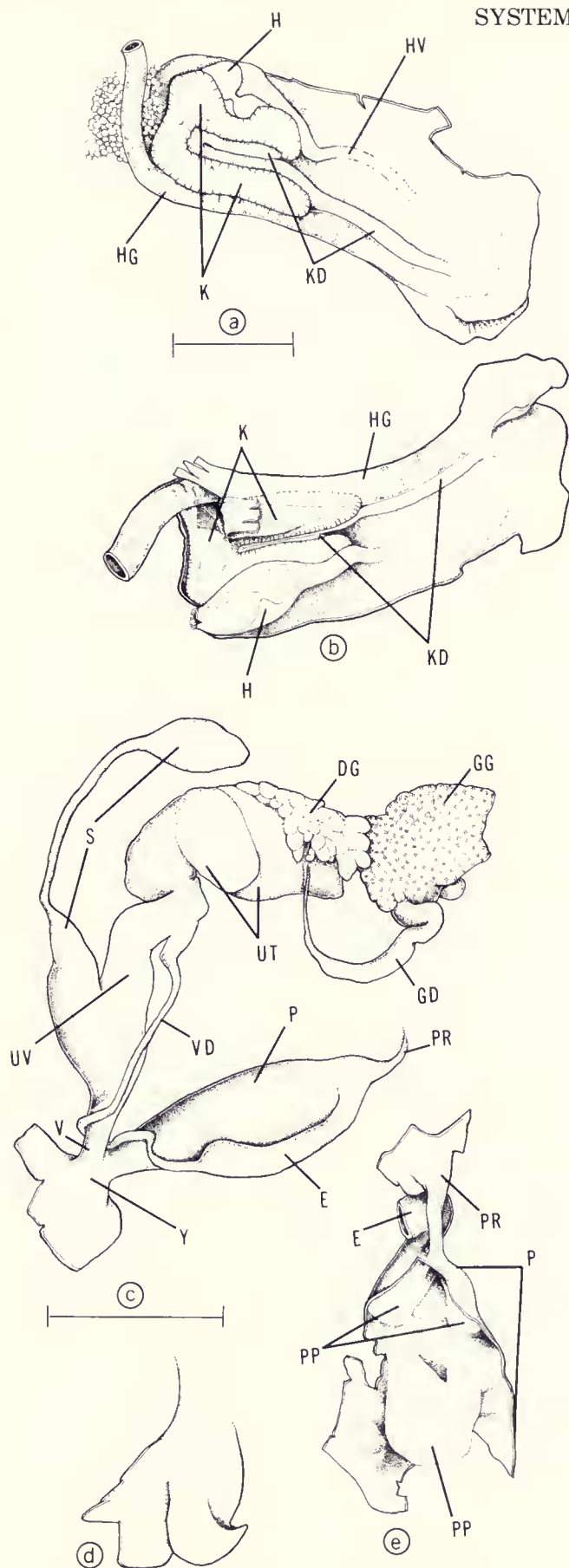


FIG. 55. Anatomy of *Sinployea allecta allecta* (Cox). Station 38, Vailoa, Savai'i, Samoa. FMNH 153091. a, external view of pallial region; b, internal view of pallial region; c, genitalia; d, mantle collar at parietal-palatal angle showing lobe development; e, interior of penis. Scale lines equal 1 mm. (MM).

gland, shaft very slender, joined by hermaphroditic duct just below head expansion. Prostate (DG) of few large acini opening into a groove on upper uterine chamber wall. Uterus (UT) bipartite, upper chamber very thin-walled, lower with thick, glandular surface.

Vas deferens (VD) reflexing up from penioviducal angle, entering epiphallus (E) through a "valve" pilaster (fig. 55e). Epiphallus more than half the length of penis, entering penis apically. Penial retractor (PR) arising on diaphragm, inserting in "U" around epiphallus-penis junction on side opposite epiphallic ascension. Penis (P) 1.3–1.5 mm. long, not tapering basally. Internally (fig. 55e) with vergic papilla enlarged and elongated, fastened to muscular collar on one side, opening to epiphallus occupying small portion of length. Main stimulatory pad lower and less sharply outlined than in most species. Atrium (Y) narrow and relatively short, without clear pilaster arrangement.

Free oviduct (UV) with thick muscular walls, internally with very narrow channel. Spermatheca (S) with expanded head lying next to albumen gland, expanded basally with same pilaster arrangement found in *S. complementaria*. Vagina (V) as in *S. complementaria*.

Free muscle system without unusual features.

Buccal mass elongately oval, small generative sac. Buccal retractors not split, inserting on lower posterior margin of buccal mass. Esophagus a narrow tube extending just apicad of pallial cavity. Stomach extending  $\frac{3}{4}$  whorl apically, anterior expansion very sudden. Intestinal looping normal, compressed into less than  $\frac{1}{2}$  whorl.

Salivary glands uniting posteriorly above esophagus.

(Based on FMNH 153091, 5 adult, expanded examples, 3.16–3.29 mm. in diameter, with  $4\frac{1}{8}$ – $4\frac{3}{8}$  whorls.)

#### *Sinployea allecta tauensis*, new subspecies. Figure 54d–e.

**Diagnosis.**—Shell slightly larger than average, diameter 2.70–3.39 mm. (mean 3.00 mm.), with  $3\frac{3}{4}$ – $4\frac{1}{4}$  somewhat tightly coiled whorls. Apex and spire noticeably and evenly elevated, body whorl descending much more rapidly, spire protrusion more than  $\frac{1}{6}$  body whorl width, H/D ratio 0.541–0.616 (mean 0.577). Apical whorls worn in all material, traces of fine spiral cords visible in most. Post-nuclear whorls with fine, low, rounded, protractively sinuated radial ribs, 61–101 (mean 79.8) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 6.20–10.51 (mean 8.31). Microsculpture of extremely fine radial riblets, 6–12 between each pair of major ribs, crossed by even finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus narrow, V-shaped, last whorl decoiling more rapidly, contained 4.72–9.55 times (mean 6.80) in the diameter, margins rounded. Whorls almost evenly rounded, not or only slightly flattened laterally above periphery.

The nominate race of *Sinployea allecta* (fig. 54b–c) has a narrower umbilicus and slightly lower spire than *S. a. tauensis* (fig. 54e–f). The only Polynesian species apt to be confused with this is the Cook Island *S. avanaensis* (fig. 45d–f), which is much less elevated and has a wider umbilicus.

**Description.**—Shell rather large, with slightly more than 4 rather tightly coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, H/D ratio 0.545. Embryonic whorls  $1\frac{1}{8}$ , sculpture of fine spiral cords visible in suture, eroded over most of surface. Postnuclear whorls with prominent, rounded, variably spaced, protractively sinuated radial ribs, 76 on the body whorl, whose interstices are 2–4 times their width, and which become very irregular near aperture. Microsculpture of extremely fine radial riblets, 5–12 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. No secondary spiral cording visible at 96 $\times$  magnification. Sutures deep, whorls evenly rounded on outer margins. Umbilicus narrow, V-shaped, last whorl decoiling more rapidly, contained 5.94 times in the diameter, slightly narrowed by columellar lip expansion. Color reddish horn on spire, last whorl separating into basal zones and

broad, irregular, sinuated reddish flammulations that coalesce on shell base. Aperture almost circular, with evenly rounded outer margins, inclined about 20° from shell axis. Height of holotype 1.81 mm., diameter 3.32 mm.

*Holotype*.—Samoa: Ta'u, Station 188, Faleasao, 700 ft. inland at 12 ft. elevation. Collected by Wray Harris on September 24, 1937. BPBM 187753.

*Range*.—Ta'u, Manu'a Group, American Samoa.

*Paratypes*.—Ta'u: Talavagi ridge and summit (Station 75) from 1/2–1/8 mile inland at 450–500 ft. elevation (4 specimens, BPBM 171106, BPBM 181998, BPBM 182095); Siufaga (Stations 76, 184), 250–600 ft. inland at 400–600 ft. elevation (12 specimens, BPBM 171073, BPBM 182055, BPBM 182400, BPBM 182410, BPBM 182444, BPBM 187635, BPBM 187640, BPBM

187653); Maia (Station 87), 1/2 mile inland at 75 ft. elevation (1 specimen, BPBM 182364); Faleasao (Stations 188, 189), 600–700 ft. inland at 12 ft. elevation (8 specimens, BPBM 187766, BPBM 187781, BPBM 187788, BPBM 188357, ex BPBM 187736, ex BPBM 188277).

*Remarks*.—All known material consists of dead specimens sorted from rubble sweepings. Normally a higher spire and narrower umbilicus are correlated changes, so that the more protruded spire and wider umbilicus of *Sinployea allecta tauensis*, compared with the nominate race, are doubly significant. Rib spacing and counts in *S. a. tauensis* are very similar to those found in the Savai'i population and rather different from the Upolu examples (table XXVI).

TABLE XXVI. — LOCAL VARIATION IN SAMOAN SINPLOYEA, II.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>allecta tauensis</u>					
Faleasao	7	77.3±4.18 (66-95)	1.76±0.048 (1.61-1.97)	3.05±0.076 (2.76-3.32)	0.577±0.0096 (0.542-0.606)
Siufaga	4	88.7±7.89 (74-101)	1.72±0.059 (1.61-1.88)	3.04±0.141 (2.70-3.39)	0.566±0.0120 (0.543-0.598)
<u>intermedia</u>					
BPBM 186666	14	81.7±4.93 (65-96)	2.03±0.032 (1.82-2.19)	3.49±0.042 (3.21-3.81)	0.581±0.0062 (0.534-0.616)
<u>complementaria</u>					
Sta. 39, 2000' FMNH 153386,-419	8	66.3±1.67 (59-73)	2.33±0.062 (2.11-2.57)	4.71±0.150 (4.31-5.20)	0.497±0.0113 (0.458-0.543)
Sta. 18, 600-800' FMNH 153016,-24, -168,-176,-557	37	69.9±1.24 (54-87)	2.43±0.025 (2.11-2.70)	4.81±0.038 (4.34-5.23)	0.505±0.0040 (0.464-0.563)
Sta. 26, 2450-2500' FMNH 153047,-99	8	62.9±2.40 (58-78)	2.73±0.070 (2.53-3.03)	5.11±0.124 (4.57-5.53)	0.534±0.0117 (0.473-0.561)
Sta. 24, 2300' FMNH 153619	3	53.0±1.00 (52-55)	2.82±0.105 (2.63-2.99)	5.21±0.090 (5.03-5.33)	0.541±0.0110 (0.523-0.562)
Sta. 13, 750' FMNH 153380,-408	5	79.8±2.98 (73-88)	2.83±0.119 (2.47-3.09)	5.32±0.217 (4.57-5.92)	0.532±0.0124 (0.506-0.577)

TABLE XXVI, CONTINUED

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>all.tau</u>				
Faleasao	4+(3 7/8-4 1/4)	0.49±0.047 (0.36-0.69)	6.45±0.515 (5.53-8.45)	-----
Siufaga	4-(3 3/4-4 1/8)	0.44±0.049 (0.33-0.56)	7.14±0.483 (6.06-8.20)	-----
<u>intermed.</u>				
BPBM	4 3/8+(4 1/4-4 3/4)	0.64±0.019 (0.53-0.79)	5.43±0.123 (4.59-6.12)	10.1±0.31 (8-12)
<u>compleme.</u>				
Sta. 39	4 5/8-(4 1/2-4 7/8)	0.93±0.046 (0.76-1.18)	5.13±0.149 (4.61-6.00)	-----
Sta. 18	4 5/8+(4 3/8-5)	0.99±0.016 (0.82-1.15)	4.89±0.060 (4.18-5.77)	9.82±0.48 (8-13)
Sta. 26	4 7/8-(4 1/2-5 1/4)	1.01±0.052 (0.82-1.22)	5.14±0.202 (4.22-6.08)	13
Sta. 24	5-(4 3/4-5)	0.99	5.28±0.160 (5.10-5.40)	-----
Sta. 13	4 7/8-(4 5/8-5)	1.07±0.662 (0.92-1.18)	4.97±0.109 (4.61-5.29)	-----



***Sinployea complementaria*** (Mousson, 1865). Figures 56a–f, 57a–f.

*Patula complementaria* Mousson, 1865, J. de Conchyl., 13, pp. 168–169, 431, pl. 14, fig. 5—Upolu, Samoa; Mousson, 1869, J. de Conchyl., 17, p. 333; Garrett, 1887, Proc. Acad. Nat. Sci., Philadelphia, 1887, pp. 129–130—behind Apia, Upolu, Samoa.

*Helix complementaria* (Mousson), Pfeiffer, 1868, Monog. helic. viv., 5, p. 157; Pfeiffer, 1876, Monog. helic. viv., 7, p. 164.

*Pityis complementaria* (Mousson), Pease, 1871, Proc. Zool. Soc. London, 1871, p. 474.

*Helix (Patula) complementaria* (Mousson), Tryon, 1887, Man. Conchol., (2) 3, pp. 40–41, pl. 8, fig. 57.

*Endodonta (Charopa) complementaria* (Mousson), Pilsbry, 1894, Man. Conchol., (2) 9, p. 35.

**Diagnosis.**—Shell extremely large, diameter 4.31–5.92 mm. (mean 4.92 mm.), with 4¼—5¼ normally coiled whorls. Apex and early spire barely to strongly elevated, last whorl usually descending much more rapidly, spire protrusion quite variable, usually about ½ body whorl width, H/D ratio 0.458–0.648 (mean 0.517). Apical sculpture of 8–13 (mean 10.08) fine spiral cords, frequently eroded. Postnuclear whorls with high, narrow, prominent, strongly protractively sinuated radial ribs, 52–95 (mean 69.1) on the body whorl, whose interstices are 3–7 times their width. Ribs/mm. 3.11–5.79 (mean 4.50). Microsculpture of extremely fine radial riblets, 9 to more than 20 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus open, V-shaped, last whorl decoiling more rapidly, contained 4.18–6.08 times (mean 4.99) in the diameter, margins rounded. Whorl contour slightly more rounded than average, flattened laterally above periphery, slightly on basal margin, aperture inclined about 20° from shell axis.

The extremely large size, comparatively few radial ribs, and a high number of microradial riblets effectively separate even juvenile examples of *Sinployea complementaria* (fig. 56a–f) from the other Samoan species. Of the larger Rarotongan species, only *S. tenuicostata* (fig. 50d–f), which has a flat spire, fewer and larger microradial riblets plus never more than 4½ whorls, might be confused. The Tongan *Tuimalila* (fig. 78a–f) are even larger, but the looser whorl coiling and reduced apical sculpture of that genus readily separates them.

**Description.**—Shell very large, with slightly more than 4¼ normally coiled whorls. Apex barely emergent, whorls of spire descending rapidly, H/D ratio 0.648. Apical whorls 1½, sculpture eroded. Postnuclear whorls with narrow, moderately widely spaced, protractively sinuated radial ribs, 73 on the body whorl, whose interstices are 3–5 times their width. Microsculpture a lattice of very fine and crowded radial riblets crossed by distinctly finer and slightly more crowded spiral riblets. No secondary spiral cording. Sutures moderately impressed, whorls slightly shouldered above, strongly flattened laterally above periphery and on basal margin. Umbilicus V-shaped, narrow, partially closed by reflection of basal lip, contained 6.00 times in the diameter. Color light yellow-brown with irregular reddish flammulations, generally parallel to the line of growth. Aperture subcircular, flattened laterally above periphery and on basal margin, inclined about 15° from the shell axis. Edge of lip broken. Height of lectotype 3.32 mm., diameter 5.14 mm.

**Lectotype.**—Samoa: Upolu. Collected by Graeffe. Zoologisches Museum der Universität Zurich.

**Range.**—Upolu, Western Samoa.

**Paratypes.**—Zurich.

**Material.**—Samoa (2 specimens, BPBM 161): Upolu (14 specimens, Zurich, IRB); foot of Mt. Solaua (Station 18) at 600–800 ft. elevation on stilts of *Ficus* or under fallen bark and rotting wood (59 specimens, FMNH 153016, FMNH 153024, FMNH 153165,

FMNH 153168, FMNH 153176, FMNH 153557); Fagaloa Pass (Station 13) at 750 ft. elevation along ridge crest under rotting wood (6 specimens, FMNH 153380, FMNH 153408); Le Mafa Pass at 900 ft. elevation under birdnest fern (2 specimens, DMW M-4002, collected by R. A. Cumber on February 10, 1955); top of range (Station 39), Mt. Solaua at 2,000 ft. elevation in heavy forest (18 specimens, FMNH 153386, FMNH 153419); Afiamalu, 6 miles inland at 2,100 ft. elevation (3 specimens, BPBM 186029, BPBM 186214); ¾ mile above Afiamalu seismographic station (Stations 2, 8) in secondary forest (2 specimens, FMNH 153050, FMNH 153089); south slope, Mt. Siga'ele (Station 24) at 2,300 ft. elevation in heavy forest (3 specimens, FMNH 153619); Afiamalu-Lake Lanuto'o track (Station 26) at 2,450–2,500 ft. elevation under rotting wood in heavy forest (9 specimens, FMNH 153047, FMNH 153099); rim of Lake Lanuto'o crater (Station 19) at 2,500 ft. elevation under dead leaves and rotting wood (18 juvenile specimens, FMNH 153133, FMNH 153424).

**Remarks.**—The lectotype is the highest specimen seen, but closely matches the type figures and has the characteristic sculpture well preserved. Spire elevation in the juvenile example (fig. 56e) is slightly less than average.

Samples collected in 1965 showed rather considerable variation, some of which may be environmentally correlated. The very large shells (table XXVI) from Fagaloa Pass come from an area of very high rainfall that also is continually swept by a moist sea breeze. Hence humidity would remain continually high, and conditions for growth would be exceptionally favorable. Specimens from Mt. Siga'ele (Station 24) were taken under litter in heavy fog forest. Their low rib count and wide rib spacing may reflect the constancy of this niche. Only juvenile examples were taken on the rim of Lanuto'o crater (Station 19). Almost all examples from Station 18 at the foot of Mt. Solaua were collected around the base of a single huge *Ficus* that was isolated from the forested slopes by a partly overgrown banana patch. Specimens of *Sinployea complementaria* were most frequent under starting bark on stilt roots from 2–5 ft. above ground level. A number were taken from under accumulated debris in the center of this tree, and only a few under fallen branches lying in grass beneath the canopy spread. None were found in the banana patch or lower forest reaches. Collecting 1,200 ft. higher on top of Mt. Solaua (Station 39) produced specimens essentially identical in measurements (table XXVI) and ribbing.

Without much more material, the question of geographic variation cannot be settled. The size difference between the Mt. Solaua and Fagaloa or Siga'ele specimens is large and significant, but there is no obvious geographic pattern. The occurrence of *S. complementaria* is strictly colonial, the specimens from Mt. Solaua, Fagaloa, and the Lake Lanuto'o areas having been obtained in a fraction of the collecting time devoted to the Afiamalu area with its two examples. *Sinployea complementaria* was found in both pro-

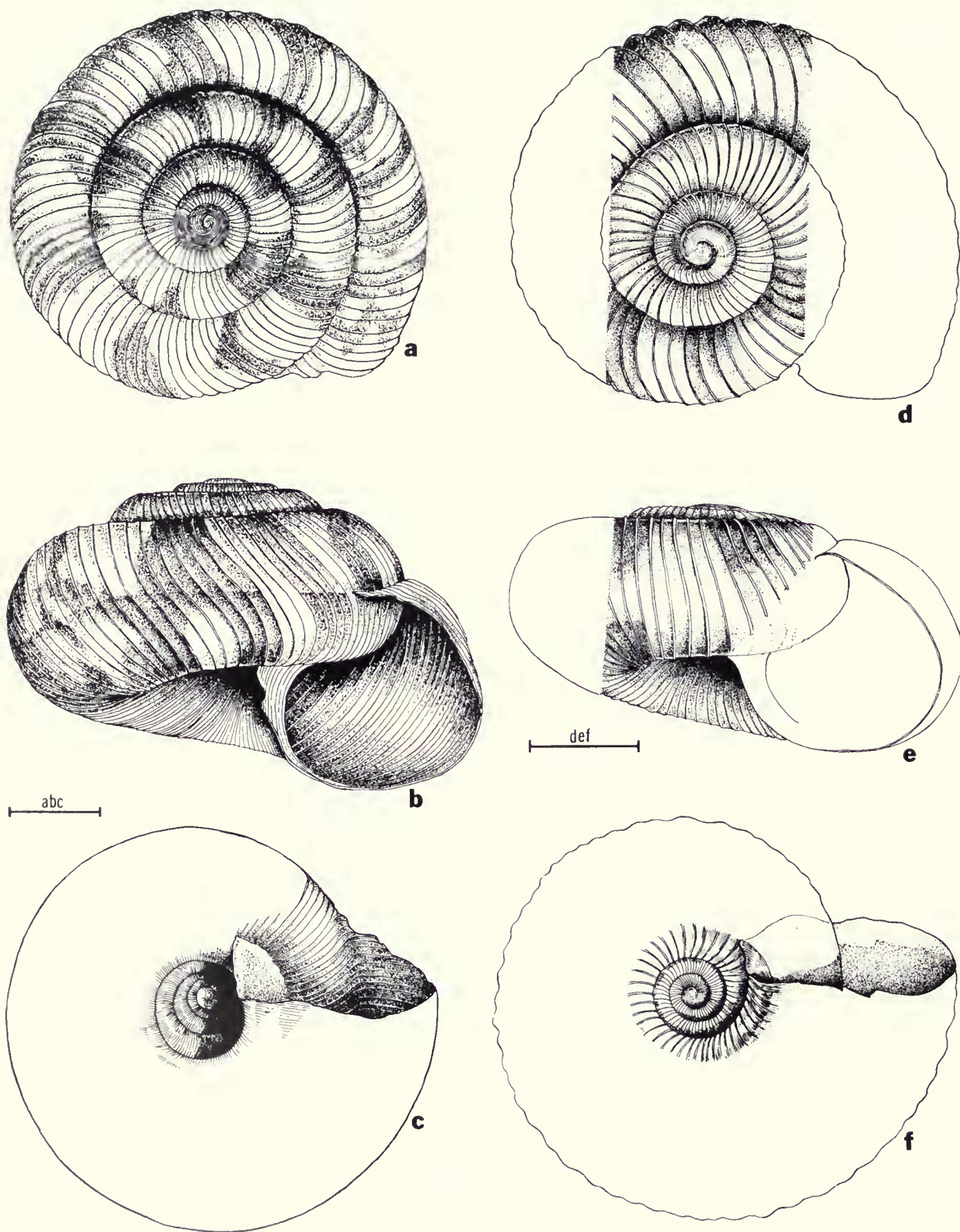


FIG. 56. *Sinployea complementaria* (Mousson). a-c, Upolu, Samoa. Lectotype of *Patula complementaria* Mousson, 1865. Zoologisches Museum Universität Zurich; d-f, Afiamalu, 2,100 ft., Upolu, Samoa. Juvenile. BPBM 186214. Scale lines equal 1 mm. (SG).



foundly disturbed (Fagaloa and foot of Mt. Solaua) and undisturbed vegetation zones.

*Description of soft parts.*—Foot and tail equal in length to shell diameter, slightly tapering posteriorly, truncated anteriorly. Sole undivided, pedal grooves high on foot, suprapedal weaker, no caudal horn or middorsal groove. Slime network typical. Gonopore a long, vertical slit behind right rhinophore and below right ommatophore.

Body color yellow-white, with light gray speckling on head and neck, ommatophores not darker.

Mantle collar (MC) swollen and rolled, no glandular extension onto pallial roof, a dark gray streak on expanded portion. Pneumostome masked by expansion of collar, no mantle lobe development. Anus (A) and external ureteric pore (KX) opening beside each other just inside pneumostome.

Pallial region (fig. 57a) extending  $\frac{3}{4}$  whorl apically. Lung roof with black specklings along edges of pulmonary vein, otherwise clear. Kidney (K) bilobed, 2.57 mm. long, rectal arm slightly longer than pericardial and crossing hindgut onto parietal wall. Ureter (KD) typical, a narrow strip of lung roof visible between arms. Heart (H) slightly more than  $\frac{1}{2}$  length of kidney, angled to hindgut. Principal pulmonary vein (HV) unbranched, fading out just short of mantle collar. Hindgut (HG) deflecting from parietal-palatal margin just before end of kidney.

Ovotestis (fig. 57b, G) a single clump of palmately clavate alveoli, lying parallel to whorl sides, occupying  $\frac{1}{3}$  whorl above stomach apex. Hermaphroditic duct (GD) slender at first, expanded and iridescent in middle, markedly kinked just before albumen gland, embedded and narrow before talon. Albumen gland (GG) with rather large acini, surface indented by intestinal loops and spermathecal head. Talon (fig. 57d, GT) with globular head, hermaphroditic duct inserting at base. Carrefour imbedded, a slightly expanded tube from neck of talon, opening into prostate-uterus. Prostate (DG) of large acini opening into groove on side of uterus, acini complexly folded. Uterus (UT) bipartite, upper chamber with very thin walls.

Vas deferens (VD) a broad tube with heavily glandular walls to penioviducal angle, where it narrows abruptly to ascend along side of penis. Epiphallus (E) large, twisted, entering head of penis laterally, with a peculiar Y-shaped valve (fig. 57e) at entrance of vas deferens, lower portion with glandular pilasters, entering penis laterally on head (fig. 57c). Penial retractor (PR) short, thick, arising on diaphragm, inserting onto head of penis. Penis (P) about 1.75–1.85 mm. long, club-shaped, gradually tapering to atrium, internally (fig. 57c) with large verge (PV) through which epiphallal pore (EP) enters medially, a reduced sphincter pilaster and a moderately large, typical pocket pilaster. Atrium (Y) of average length, with weak longitudinal pilasters.

Free oviduct (UV) a long, thick muscular tube with an apical muscle attaching to right tentacular retractor, internally (fig. 57f) with heavy glandular walls ending in a hemispherical protrusion with subcentral pore (UVO) just at junction with spermathecal base, externally smoothly muscled. Spermatheca (S) with head lying next to albumen gland, slender shaft bound to diaphragm tissue to base of uterus, then grossly expanded to vagina level, with complex pilasters forming a circular ring at area of vagina, with a flap obviously capable of closing the spermathecal opening (SO). Vagina (V) quite thin-walled, with weak internal pilasters.

Free muscle system typical, muscle from free oviduct quite prominent. Right ommatophoral retractor passing through penioviducal angle.

Buccal mass and esophagus without unusual features. Stomach occupying a little more than  $\frac{3}{4}$  whorl, shape and expansion typical. Intestinal looping occupying less than  $\frac{1}{8}$  whorl above pallial cavity apex.

Salivary glands fused across top of esophagus.

Central tooth of radula distinctly smaller than 1st lateral, tricuspid with mesocone extending anterior to basal plate edge. Laterals 4–5, with endocone increasing regularly, transitions to marginals marked by shift in support size and increasing size of endocones.

Marginals 6–7, outer ones with endocone and mesocone subequal, ectocone always much smaller, no evidence of ectoconal splitting.

(Based on FMNH 153165, 4 whole individuals, 4.9–5.1 mm. in diameter.)

### *Sinployea intermedia*, new species. Figures 52d–f, 53f–h.

*Diagnosis.*—Shell large, diameter 3.21–3.81 mm. (mean 3.49 mm.), with  $4\frac{1}{4}$ – $4\frac{3}{4}$  rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion about  $\frac{1}{5}$  body whorl width, H/D ratio 0.534–0.616 (mean 0.581). Apical sculpture of 9–13 (mean 10.57) very fine spiral cords. Postnuclear whorls with low, rounded, prominent, protractively sinuated radial ribs, 63–96 (mean 82.1) on the body whorl, whose interstices are usually 3–5 times their width. Ribs/mm. 5.75–9.16 (mean 7.66). Microsculpture of fine radial riblets, 5–10 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 4.59–6.12 times (mean 5.43) in the diameter, margins rounded. Whorls only slightly flattened laterally above periphery, strongly rounded on basal margin.

*Sinployea intermedia* (fig. 52d–f) has a distinctly more protruded spire, wider umbilicus, slightly greater number of apical cords and is larger than any of the *S. allecta* (fig. 54a–e) races. Society and Cook Island species of the same size are more widely umbilicated and have quite different ribbing structure.

*Description.*—Shell larger than average, with slightly more than  $4\frac{1}{2}$  moderately tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending more rapidly, H/D ratio 0.592. Embryonic whorls  $1\frac{1}{2}$ , sculpture of 8 relatively weak spiral ribs with irregularly radially ribbed last quarter whorl. Remaining whorls with low, rounded, moderately widely spaced, protractively sinuated radial ribs, 90 on pregerontic portion of body whorl, whose interstices are about 2–3 times their width. Microsculpture of extremely fine microradial riblets, 5–10 between each pair of major ribs, and smaller microspiral riblets forming a latticed pattern. Sutures relatively deep, whorls strongly rounded above and on basal margin, body whorl slightly deflected at aperture. Umbilicus narrowly U-shaped, becoming more widely open on last whorl, contained 4.91 times in the diameter. Color light yellowish white with numerous irregular reddish flammulations. Aperture circular, slightly compressed laterally above periphery by deflection of lip, inclined about  $15^\circ$  from the shell axis. Height of holotype 2.11 mm., diameter 3.56 mm.

*Holotype.*—Swains Island: 200 yd. inland on west side at 20 ft. elevation. Collected under coconut husks and fallen limbs by Elwood C. Zimmerman on August 21, 1940. BPBM 186666.

*Range.*—Swains Island, American Samoa.

*Paratypes.*—Swains Island: west side, 200–500 yd. inland at 20 ft. elevation (45 specimens, BPBM 186666–8, BPBM 186679).

*Remarks.*—Differences from *Sinployea allecta* are adequately covered in the diagnosis above. Although closely related to that species, I have no doubt that *Sinployea intermedia* is distinct. Presence of an endemic species on Swains Island, a very isolated but heavily vegetated atoll, was unexpected. Swains Island is less than 20 ft. high and not over  $1\frac{1}{2}$  mile in greatest dimension (Bryan, 1942, p. 83).

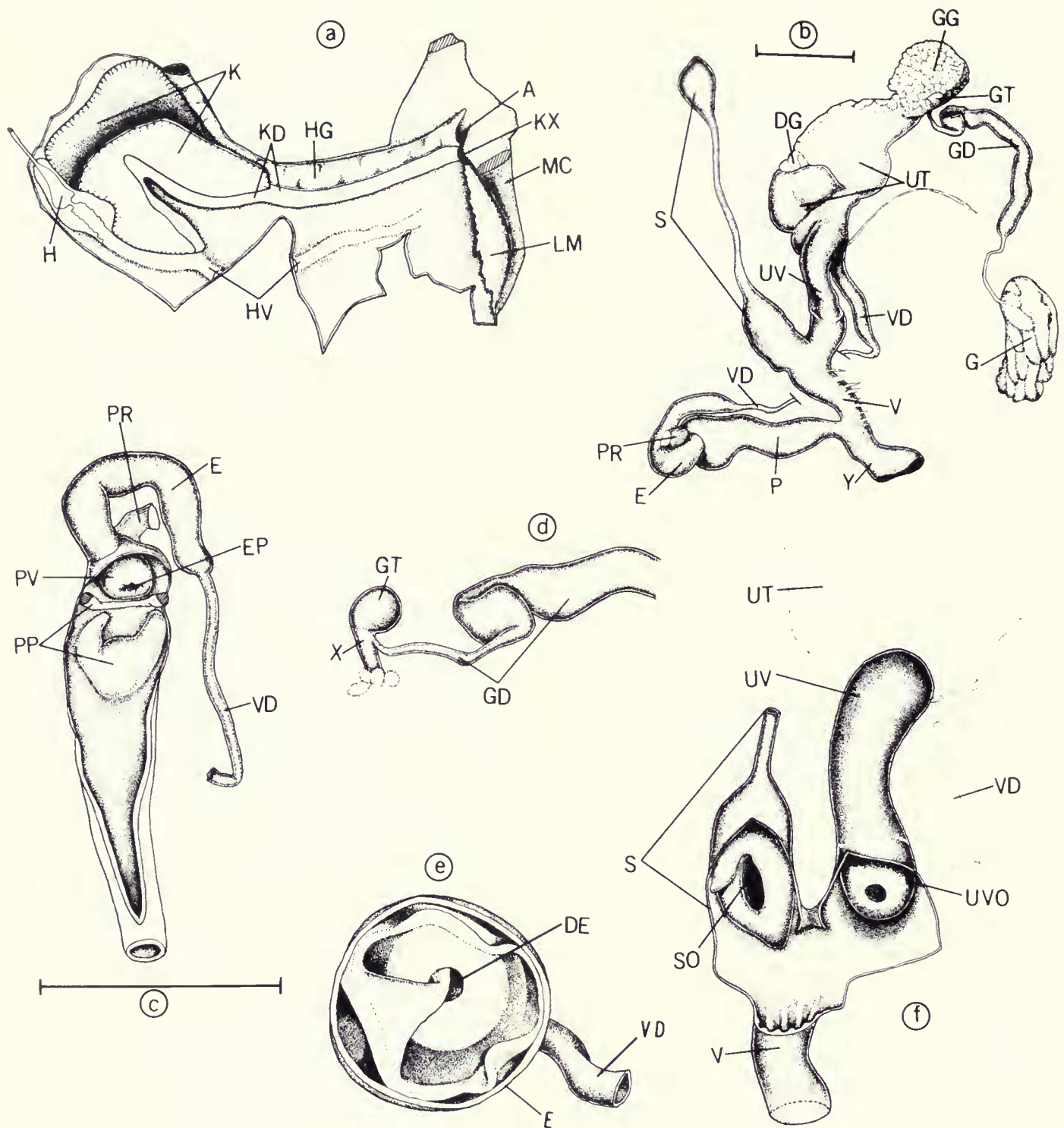


FIG. 57. Anatomy of the Samoan *Sinployea complementaria* (Mousson). Station 18, Mt. Solaua, Upolu, Samoa. FMNH 153165: a, pallial region; b, genitalia; c, interior of penis; d, detail of talon-carrefour area; e, junction of vas deferens and epiphallus; f, interior of spermatheca and free oviduct junction. Scale lines equal 1 mm. (SH).

*Description of soft parts.*—Foot and tail shorter than shell diameter. Sole undivided, slightly tapering posteriorly. Pedal grooves high on sides of foot, prominent.

Body color light yellow-white, no grayish markings.

Mantle collar (MC) thick and swollen in available material, no glandular extension onto mantle roof.

Pallial region (fig. 53f) extended length about  $\frac{1}{2}$  whorl. Lung roof clear of granulations. Kidney (K) bilobed, rectal lobe longer than pericardial, greatest length 1.65–2.00 mm., differing from *S. allecta*

in having less overlap of hindgut and greater lung roof visible between arms of ureter (KD). Heart (H) and principal pulmonary vein (HV) typical. Hindgut (HG) following parietal-palatal margin for moderate distance above kidney apex.

Ovotestis (fig. 53g, G) composed of one or two acinar clumps in typical position. Hermaphroditic duct (GD), albumen gland (GG), talon (GT), prostate (DG), and uterus (UT) without unusual features.

Vas deferens (VD) and epiphallus (E) as in *Sinployea allecta*. Penial retractor (PR) as in *S. allecta*. Penis (P) 1.2–1.6 mm. long,



tapering more on basal portion than in *S. allecta*, externally strongly swollen on upper half. Internally (fig. 53h) with typical stimulatory pad, vergic papilla as in *S. allecta*. Atrium (Y) very short, without unusual features.

Free oviduct (UV), spermatheca (S), and vagina (V) typical; latter a trifle longer than in *S. allecta*.

(Based on BPBM 186666, several partial examples.)

#### WESTERN POLYNESIAN AND MICRONESIAN *Sinployea*

Whereas the *Sinployea* from Tonga, Hoorn Islands, Ellice Islands, and Rotuma show many similarities, inclusion of the single species from Kusaie in the Caroline Islands and a possibly introduced form from Saipan in the Marianas is merely for convenience in reducing the number of subheadings. *Sinployea kusaieana* (fig. 63a-c) lacks gray coloration on the head and ommatophores, has monochrome shell coloration, a less protruded spire, fewer and more loosely coiled whorls, and the umbilicus wider and V-shaped. Two specimens collected on Saipan could represent an introduced population, a mislabeled set, or another undescribed Micronesian species.

Of the remaining species, only *Sinployea pseudovicaria* (fig. 61a-c) with its low H/D ratio and

wide umbilicus (table XXVII) is distinctive. The Tahitian *S. lamellicosta* (Garrett) (fig. 40a-c) is virtually identical in size and shape, but has a depressed spire, averages less than half as many ribs, and has slightly fewer whorls at a given diameter. Other widely umbilicated *Sinployea* are either much bigger (*S. canalis*, fig. 49a-c), have many more whorls (*S. planospira*, fig. 46d), or are much smaller (*S. nissani*, *S. navutuensis*). *Sinployea rotumana* (E. A. Smith) (fig. 61d-f) perhaps comes closest of any species to being median in its features. Only the slightly more numerous and crowded radial ribs depart from the median measurements outlined in Table XV. *Sinployea ellicensis* (fig. 62a-f) is a rather small, normally elevated species with crowded radial ribbing. *Sinployea vicaria* (Mousson) (fig. 58a-d) is larger and with a rather elevated spire. Both of these species have less marked lateral whorl flattening than species from Eastern Polynesia. Although measurements overlap, the round apertures and generally elevated spires would allow immediate recognition in mixed sets.

Because none of the species are sympatric, no formal key has been prepared. The following geographic notes will locate material of known taxa:

TABLE XXVII. - RANGE OF VARIATION IN WESTERN POLYNESIAN AND MICRONESIAN SINPLOYEA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO		
<i>ellicensis</i>								
<i>ellicensis</i>	106	100.3(79-125)	13.23(10.55-16.69)	1.36(1.13-1.68)	2.47(2.20-2.81)	0.549(0.486-0.600)		
<i>ellicensis</i> <i>nukulaelaeana</i>	8	84.5(72-102)	13.02(11.06-15.20)	1.11(1.06-1.16)	2.08(1.99-2.20)	0.533(0.496-0.561)		
<i>vicaria</i>								
<i>vicaria</i> (Mousson)	326	108.5(77-145)	12.65(8.72-15.91)	1.51(1.17-1.89)	2.73(2.14-3.15)	0.552(0.469-0.633)		
<i>vicaria</i> <i>paucicosta</i>	87	77.1(51.98)	9.80(6.71-11.44)	1.45(1.18-1.78)	2.49(2.22-2.76)	0.585(0.500-0.659)		
<i>rotumana</i> (Smith)	9	105.2(84-144)	11.74(9.79-14.15)	1.55(1.25-1.81)	2.84(2.60-3.24)	0.547(0.481-0.607)		
<i>pseudovicaria</i> Vaitupu	21	108.1(82-127)	11.39(9.56-15.17)	1.57(1.41-1.74)	3.24(3.03-3.52)	0.486(0.454-0.525)		
Eua (?)	7	94.8(81-113)	8.93(8.43-9.77)	1.61(1.45-1.74)	3.37(3.06-3.68)	0.479(0.455-0.509)		
<i>kusaieana</i>	61	91.1(84-103)	11.25(10.27-13.12)	1.32(1.19-1.49)	2.60(2.52-2.75)	0.506(0.462-0.542)		
<i>sp.</i> (Saipan)	2	85.0(82-88)	11.44(11.20-11.67)	1.41(1.38-1.45)	2.37(2.34-2.40)	0.598(0.592-0.603)		
	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW	
<i>e.ell.</i>	4 1/8(4-4 1/2)	0.56(0.43-0.76)	4.39(3.48-5.46)	9.42(8-12)	0.15(0.10-0.23)	0.82(0.72-0.92)	0.183(0.125-0.259)	
<i>e.nuk.</i>	3 7/8+(3 5/8-4)	0.48(0.44-0.59)	4.31(4.13-4.66)	11.67(11-13)	0.11(0.10-0.16)	0.68(0.64-0.72)	0.166(0.136-0.250)	
<i>v.vic.</i>	4 1/4(3 3/4-4 3/4)	0.58(0.41-0.75)	4.47(3.88-5.80)	10.63(9-12)	0.21(0.10-0.38)	0.86(0.69-1.02)	0.251(0.111-0.417)	
<i>v.pau.</i>	4 1/2(4 1/4-5)	0.69(0.49-0.72)	4.14(3.62-4.64)	11.50(10-12)	0.21(0.10-0.33)	0.79(0.69-0.89)	0.268(0.125-0.385)	
<i>rotum.</i>	4 1/4(4-4 5/8)	0.66(0.58-0.81)	4.32(3.93-4.86)	9.67(8-11)	0.17(0.07-0.25)	0.95(0.84-1.04)	0.175(0.073-0.268)	
<i>pseud.</i>								
Vait.	4 3/8+(4 1/4-4 5/8)	1.03(0.79-1.22)	3.17(2.89-4.05)	11.74(10-13)	0.10(0.07-0.13)	0.86(0.79-0.95)	0.121(0.083-0.160)	
Eua	4 1/2(4 1/4-4 3/4)	1.08(0.99-1.25)	3.13(2.95-3.30)	----	----	----	----	
<i>kusai.</i>	3 7/8+(3 3/4-4 1/8)	0.74(0.69-0.79)	3.51(3.21-3.67)	9.20(8-10)	0.12(0.10-0.16)	0.79(0.72-0.86)	0.150(0.125-0.208)	
<i>sp.</i>	3 7/8+	0.53(0.49-0.56)	4.52(4.30-4.73)	----	----	----	----	

Tonga and Hoorn Islands: *S. vicaria* (Mousson, 1871)

*Sinployea vicaria paucicosta*, new subspecies  
on southern Vava'u

Rotuma Island: *S. rotumana* (E. A. Smith, 1897)

Ellice Islands—

Vaitupu: *S. pseudovicaria*, new species  
(widely umbilicated)

Funafuti: *S. ellicensis ellicensis*, new sub-  
species

Nukulaelae: *S. ellicensis nukulaelaeana*, new  
subspecies

Caroline Islands—

Kusaie: *S. kusaieana*, new species

Mariana Islands—

Saipan: *Sinployea* sp.

### *Sinployea vicaria* (Mousson, 1871).

Several small samples from scattered islands of the Tonga and Hoorn group collected by Graeffe in the 1860s and 1870s, plus material from Vava'u, Tongatapu, and Eua collected by L. Price in 1966 agree closely in proportions (table XXVIII). Four samples from Vava'u have a distinctive pattern of more widely spaced ribbing and are separated as a subspecies, *Sinployea vicaria paucicosta* (fig. 58d). Size differences among the remaining samples may be attributed to sample bias and/or ecophenotypic dwarfing (p. 108). They are grouped as a single subspecies. It is quite possible that more ample material, particularly from Futuna, will cause a revision in this judgment.

General appearance and sculpture are much more similar to the smaller Cook Island *Sinployea*, *S. atiensis*, *S. andrewi*, and *S. peasei*, than to any of the Samoan or Fijian species.

### *Sinployea vicaria vicaria* (Mousson, 1871). Figures 58a-c, 60a-d.

*Patula* (*Patula*) *vicaria* Mousson, 1871, J. de Conchyl., 19, pp. 11-12, pl. 3, fig. 2—Futuna, Hoorn Group; Hufena on Hapai (probably is Uoleva Id., Haapai Group) and Vavao, Tonga Islands.

*Helix vicaria* (Mousson), Pfeiffer, 1876, Monog. helic. viv., 7, p. 187.

*Helix modicella* (Férussac), Tryon, 1887, Man. Conch., (2) 3, p. 38, pl. 8, figs. 31-32.

*Rhytida* (*Ouagapia*) *vicaria* (Mousson), Möllendorff, 1903, Syst. Conchyl. Cab., I, 12b, pp. 83-84, pl. 13, figs. 16-17.

**Diagnosis.**—Shell variable in size, generally slightly smaller than average, diameter 2.14-3.15 mm. (mean 2.73 mm.), with 3¼-4¼ rather tightly coiled whorls. Apex and spire markedly and almost evenly elevated, last whorl descending moderately to much more rapidly, spire protrusion averaging ¼ body whorl width, H/D ratio 0.469-0.633 (mean 0.552). Apical sculpture of 9-12 (mean 10.63) very fine spiral cords. Postnuclear whorls with narrow, rounded, crowded, rather strongly protractively sinuated radial ribs, 77-145 (mean 108.5) on the body whorl, whose interstices are 1-3 times their width. Ribs/mm. 8.72-15.91 (mean 12.65). Microsculpture of very fine radial riblets, 5-8 between each pair of major ribs, barely visible microspiral riblets, and rather closely spaced secondary spiral cords equal in size to microradial riblets. Umbilicus rather narrow, U-shaped, last whorl decoiling more rapidly, contained 3.88-5.80 times (mean 4.47) in the diameter, margins rounded. Whorls less strongly flattened laterally than in Society or Cook Island species.

*Sinployea vicaria* (table XXVII) is very similar to *S. atiensis* (table XIX) in all measurements, differing only slightly in ribbing and umbilical coiling. In *S. atiensis* (fig. 44d-f) the umbilicus decoils regularly, the secondary spiral cording is noticeably wider spaced, and the whorl contour is more strongly flattened laterally. *Sinployea vicaria* (fig. 58a-c) usually has a more rapid decoiling of the umbilicus and slightly more crowded ribbing. *Sinployea pseudovicaria* (fig. 61a-c) is immediately separable by its nearly flat spire and much more widely open umbilicus. *Sinployea rotumana* (fig. 61d-f) has the body whorl strongly flattened laterally and more crowded secondary spiral cording. *Sinployea neglecta* (fig. 41d-f) has finer ribs, fewer microradial riblets, a V-shaped umbilicus, and greater lateral whorl flattening.

**Description.**—Shell of average size, with 4¼ normally coiled whorls, apex barely emergent, whorls of spire descending moderately, last whorl more rapidly, H/D ratio 0.538. Apical whorls 1¾, sculpture of 11 fine, moderately widely spaced spiral ribs with a faint microsculpture of radial ribs and a secondary intrusion of radial growth wrinkles near the end. Postnuclear whorls with prominent, narrow, protractively sinuated radial ribs, 82 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of very fine radial riblets, 4-8 between each pair of major ribs, crossed by barely visible spiral riblets with a prominent secondary sculpture of closely spaced spiral cording. Sutures moderately impressed, whorls slightly flattened laterally above and below periphery with evenly rounded outer margins. Color light yellowish white with irregular somewhat vague reddish flammulations. Umbilicus V-shaped, moderately open, last whorl decoiling a little more rapidly, contained 5.05 times in the diameter. Aperture subcircular, somewhat flattened basally, inclined about 20° from shell axis. Height of lectotype 1.61 mm., diameter 3.00 mm.

**Lectotype.**—Tonga: Vava'u. Collected by E. Graeffe. Zoologisches Institut der Universität, Zurich.

**Range.**—Futuna, Hoorn Islands; Vava'u, Tongatapu, Eua, and Ha'apai Group, Tonga Islands.

**Material.**—Tonga: Vava'u (3 specimens, Zurich): Utula'aina (Station T-13) near Holonga in heavy forest at 10-100 ft. elevation (265 specimens, FMNH 152372-3); 200 yd. inland on cliffs at 200-350 ft. elevation, north side of island (4 specimens, BPBM 87859). Ha'apai Group, Hufena (= Uoleva) (4 specimens, Zurich). Eua (6 specimens, Zurich, FMNH 150773, BMNH 93.9.25.81): heavy primary forest near south end (Stations T-21, T-22) at 850-1,000 ft. elevation (5 specimens, FMNH 152519, FMNH 152379). Tongatapu: Manima Id., 4 miles northeast of Nuku'alofa (Station T-4) in second growth on a coral islet (1 specimen, FMNH 152397); about 11 miles northwest of Nuku'alofa, 200 yd. inland (Station T-26) in coastal scrub (32 specimens, FMNH 152312, FMNH 152461). Fukave, near Tongatapu (1 specimen, BPBM 53524).

Hoorn Islands: Futuna (6 specimens, Zurich, FMNH 150772).

**Remarks.**—Recorded variation between sets of *Sinployea vicaria* (table XXVIII) is quite large, with a spread of 0.75 mm. between the smallest in diameter (recent collection from Eua) and the largest (type series from Vava'u). Two factors reduce the possibility that this has any systematic significance. The specimens in the Mousson collection at Zurich were selected by



TABLE XXVIII. - LOCAL VARIATION IN *SINPLOYEA VICARIA*.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u><i>vicaria vicaria</i></u>						
Vavau Zurich	3	100.3±9.21 (82-111)	10.54±0.920 (8.72-11.61)	1.72±0.083 (1.62-1.89)	3.05±0.051 (2.98-3.15)	0.566±0.034 (0.526-0.633)
Hufena, Haapaii Zurich	4	101.0±2.68 (95-108)	11.99±0.307 (11.49-12.82)	1.60±0.045 (1.49-1.71)	2.70±0.035 (2.65-2.80)	0.593±0.0115 (0.563-0.612)
Tongatapu Sta. T-26 FMNH 152312,-461	15	118.3±3.87 (96-145)	13.34±0.369 (10.59-15.76)	1.53±0.039 (1.30-1.78)	2.82±0.050 (2.52-3.09)	0.541±0.0087 (0.469-0.596)
Fukave, Tongatapu BPBM 53524	1	128	14.40	1.51	2.83	0.535
Eua Zurich	5	105.0±2.98 (96-113)	11.84±0.381 (10.80-13.17)	1.50±0.034 (1.42-1.62)	2.84±0.049 (2.75-3.03)	0.527±0.0063 (0.511-0.547)
Sta. T-21 FMNH 152519	4	92.0±1.53 (90-95)	12.72±0.683 (11.36-13.42)	1.25±0.062 (1.17-1.43)	2.30±0.088 (2.14-2.55)	0.546±0.0166 (0.518-0.585)
BMNH 93.9.25.81	1	143	15.91	1.74	2.86	0.609
Futuna Zurich	5	96.2±6.40 (77-111)	12.20±0.442 (11.03-13.69)	1.42±0.055 (1.33-1.61)	2.50±0.094 (2.22-2.80)	0.569±0.0100 (0.546-0.600)
<u><i>vicaria paucicosta</i></u>						
Vavau Sta. T-8 FMNH 152488	10	78.0±5.85 (51-98)	9.39±0.590 (6.71-11.42)	1.51±0.041 (1.27-1.78)	2.63±0.038 (2.42-2.76)	0.574±0.012 (0.500-0.643)
Sta. T-9 FMNH 152414	28	76.8±1.68 (67-89)	9.95±0.210 (8.54-11.44)	1.43±0.018 (1.18-1.63)	2.44±0.021 (2.22-2.62)	0.589±0.0062 (0.518-0.659)
Sta. T-13 FMNH 152372-3	60	89.6±1.20 (66-108)	10.39±0.131 (8.08-12.59)	1.48±0.016 (1.25-1.81)	2.76±0.025 (2.43-3.35)	0.536±0.0032 (0.467-0.588)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE PROTRUSION	BWW	SP/BWW
<u><i>v. vicaria</i></u>							
Vavau	4 3/8+(4 1/4-4 3/4)	0.65±0.040 (0.59-0.72)	4.71±0.312 (4.09-5.05)	11	0.25±0.067 (0.16-0.38)	0.97±0.025 (0.94-1.02)	0.257±0.074 (0.161-0.404)
Hufena	4 3/8+(4 1/4-4 5/8)	0.62±0.024 (0.56-0.67)	4.33±0.130 (4.13-4.71)	10.33±0.883 (9-12)	0.28±0.032 (0.20-0.35)	0.85±0.022 (0.81-0.89)	0.335±0.038 (0.222-0.389)
Tongatapu	4 1/4-(4-4 1/2)	0.66±0.017 (0.51-0.76)	4.28±0.092 (3.88-5.26)	11.2±0.374 (10-12)	0.23±0.014 (0.16-0.33)	0.86±0.013 (0.77-0.92)	0.269±0.016 (0.189-0.417)
Fukave	4 1/8	0.66	4.30	-----	0.20	0.82	0.240
Eua Zurich	4 1/8+(4-4 1/4)	0.63±0.024 (0.56-0.61)	4.52±0.116 (4.20-4.88)	11.00±0.578 (10-12)	0.15±0.078 (0.10-0.21)	0.91±0.021 (0.87-0.99)	0.167±0.026 (0.111-0.241)
Sta. T-21	4-(3 3/4-4 1/8)	0.47±0.037 (0.41-0.57)	4.91±0.224 (4.43-5.48)	-----	0.17±0.012 (0.15-0.20)	0.72±0.022 (0.69-0.79)	0.228±0.0172 (0.208-0.279)
BMNH	4 1/4	0.49	5.80	-----	-----	-----	-----
Futuna	4 1/4+(4-4 1/2)	0.38±0.038 (0.44-0.66)	4.34±0.172 (4.03-5.00)	9.75±0.479 (9-11)	0.19±0.022 (0.13-0.26)	0.84±0.009 (0.82-0.87)	0.231±0.0199 (0.157-0.302)
<u><i>v. paucicos.</i></u>							
Sta. T-8	4 1/2+(4 1/2-5)	0.65±0.014 (0.59-0.72)	4.06±0.089 (3.62-4.54)	11.25±0.479 (10-12)	0.23±0.020 (0.15-0.33)	0.83±0.017 (0.76-0.89)	0.276±0.0243 (0.196-0.385)
Sta. T-9	4 3/8(4 1/4-4 5/8)	0.59±0.008 (0.49-0.67)	4.17±0.042 (3.73-4.64)	11.67±0.211 (11-12)	0.21±0.010 (0.10-0.33)	0.77±0.007 (0.69-0.86)	0.265±0.130 (0.125-0.360)
Sta. T-13	4 1/4-(3 3/4-4 5/8)	0.59±0.008 (0.46-0.72)	4.71±0.054 (3.90-5.71)	-----	0.16±0.006 (0.07-0.26)	0.91±0.008 (0.79-1.08)	0.181±0.0071 (0.080-0.286)

Mousson from field collections that were then deposited in the Godeffroy collection. Presumably these large specimens can be equated with the retention by Garrett of larger examples in his collection (for example see *S. proxima*, p. 108). Hence, a major part of the larger size shown by the Mousson Eua Island and Vava'u material could result from biased sampling. Second, the material collected by Price in 1966 was taken after an extended period of drought. Quite possibly, ecophenotypic dwarfing was involved in the rela-

tively small size of these shells. Since the proportions, whorl counts, and ribbing are essentially identical, I am ignoring the size differences and consider them conspecific. Inclusion of the Futuna shells is less certain, but their proportions and ribbing match the Tongan examples.

Comparison of measurements in Tables XIX and XXVII demonstrates that *Sinployea vicaria* and *S. atiensis* are extremely similar in size and proportions. Direct comparisons of specimens show that in *S. vi-*

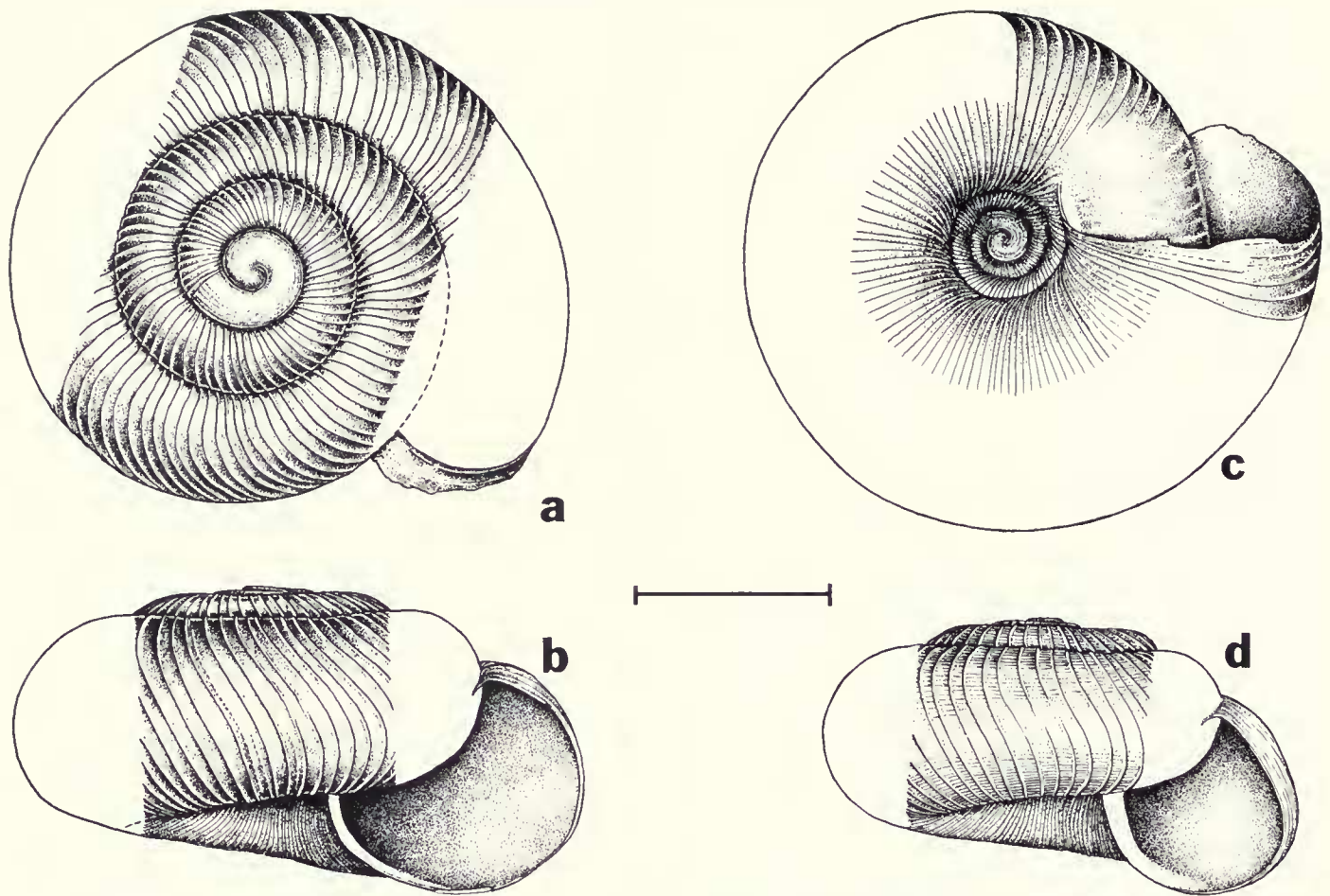


FIG. 58. a–c, *Sinployea vicaria vicaria* (Mousson). Vava'u, Tonga. Lectotype. Zoologisches Institut der Universität Zurich; d, *Sinployea vicaria paucicosta*, new subspecies. Station T-9, Mo'ungalafa, Vava'u, Tonga. Holotype. FMNH 158449. Scale lines equal 1 mm. (SH).

*caria* the secondary spiral cording is much more crowded, the apical cords reduced in prominence, the body whorl less distinctly flattened laterally above the periphery, and the last whorl of the umbilicus decoils slightly more rapidly. On the average, specimens of *S. vicaria* have about one more rib/mm. and perhaps 15 more ribs on the body whorl, but overlap is complete and these characters cannot be used to separate the taxa. The similarities are considered to be convergent and caused by the limited patterns of coiling available to these snails.

Mousson's original measurements of 3 mm. in diameter and  $4\frac{1}{2}$  whorls are most closely matched by the specimen from Vava'u selected as lectotype. It is atypical in having an umbilicus that is slightly narrower than usual because of regular last whorl decoiling (fig. 58c).

*Description of soft parts.*—Foot and tail slightly shorter than shell diameter, truncated anteriorly, bluntly rounded, and slightly tapering posteriorly. Sole undivided, pedal grooves prominent, high on foot, no caudal horn or middorsal groove developed. Slime network typical. Head projecting in front of foot, ommatophores long, dark in color. Gonopore below right ommatophore and behind right rhinophore, a vertical, short slit in body wall.

Body color yellow-white on sides and sole of foot, back of head and neck, ommatophores, and inner part of mantle collar heavily to moderately speckled with gray.

Mantle collar (MC) wide, white on outer edge, heavily marked with gray on inner edge, no glandular extension onto pallial roof. Anus (A) opening just anterior to external ureteric pore (KX).

Pallial region (fig. 60a) extending slightly less than  $\frac{1}{2}$  whorl apically. Lung roof clear, without granulations. Kidney (K) about 1.45 mm. long, rectal lobe slightly longer than pericardial. Rectal arm crossing hindgut and extending well down onto parietal wall. Ureter (KD) typical, a strip of lung roof visible between arms. Heart (H) nearly parallel to hindgut,  $\frac{2}{3}$  length of pericardial kidney lobe. Principal pulmonary vein (HV) narrow, unbranched, fading out just before mantle collar. Hindgut (HG) extending about 0.3 mm. above kidney apex before starting to deflect downward.

Ovotestis (fig. 60b) a single clump of palmately clavate alveoli above stomach apex, lying parallel to plane of coiling, sharply truncate anteriorly, soft parts extending one full whorl above ovotestis apex. Hermaphroditic duct (GD) typical. Albumen gland, talon, prostate, and uterus without unusual features.

Vas deferens (fig. 60c, VD) typical, epiphallus (E) more than half length of penis, entering penis apically through a longitudinal epiphallic pore (EP). Penial retractor (PR) short, attached in U-fan to head of penis, arising from diaphragm. Penis (P) about 1.4 mm. long, lower third very narrow, internally (fig. 60d) with distinct collar (PVS) around prominent vergic papilla (PV). Normal circular muscle collar reduced to a low ridge, main stimulatory pad quite prominent. Atrium (Y) long, medially swollen.

Free oviduct (UV) enlarging rapidly in diameter just before junction with spermatheca. Spermatheca (S) and vagina (V) typical.

(Based on FMNH 152373, several expanded adults, 2.73–2.93 mm. in diameter, with  $4\frac{1}{8}$ – $4\frac{1}{2}$  whorls.)



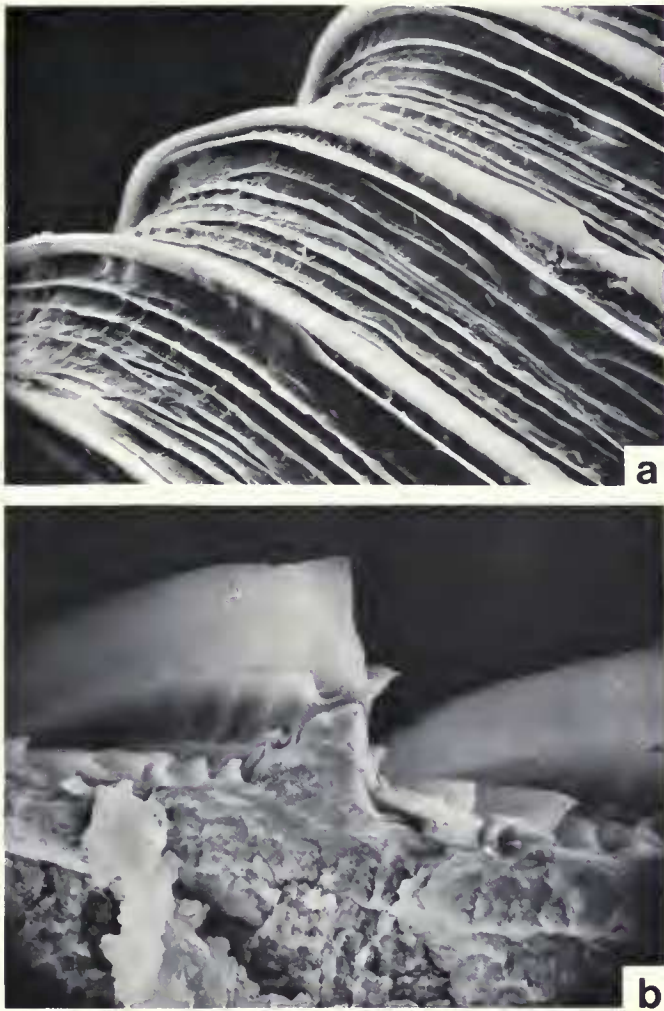


FIG. 59. Shell sculpture details of *Sinployea vicaria vicaria* (Mousson). Station T-13, Vava'u, Tonga. FMNH 152373: a, sculpture of body whorl (535 $\times$ ); b, fracture section through body whorl showing periostracal (upper) and calcareous (lower) elements of sculpture (950 $\times$ ).

***Sinployea vicaria paucicosta*, new subspecies. Figure 58d.**

**Diagnosis.**—Shell small, diameter 2.22–2.76 mm. (mean 2.49 mm.), with 4¼–5 rather tightly coiled whorls. Apex and first post-nuclear whorl barely emergent, lower whorls descending more rapidly, body whorl much more rapidly, spire protrusion slightly more than ¼ body whorl width, H/D ratio 0.500–0.659 (mean 0.585). Apical sculpture of 10–12 (mean 11.5) fine spiral cords. Postnuclear whorls with prominent, narrow, rather widely spaced, protractively sinuated radial ribs, 51–98 (mean 77.1) on the body whorl, whose interstices are 5–8 times their width. Ribs/mm. 6.71–11.44 (mean 9.80). Microsculpture of very fine radial riblets, 8–12 between each pair of major ribs, barely visible microspiral riblets, and prominent, relatively crowded secondary spiral cords. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.62–4.64 times (mean 4.14) in the diameter, margins rounded. Whorl contour and sutures as in the nominate race.

*Sinployea vicaria paucicosta* (fig. 58d) differs from the nominate race in its more sharply defined and more widely spaced ribbing. The smaller size, slightly greater H/D ratio, wider umbilicus, and average of one more apical cord are of uncertain significance. *Sinployea ellicensis* (fig. 62a–f) has much more

crowded ribbing and fewer whorls, whereas *S. pseudovicaria* (fig. 61a–c) is widely umbilicated and much larger.

**Description.**—Shell small, with 4¾ rather tightly coiled whorls. Apex barely elevated, later whorls descending much more rapidly, H/D ratio 0.595. Apical whorls and early spire with sculpture eroded. Postnuclear whorls with narrow, prominent, strongly protractively sinuated radial ribs, 69 on the body whorl, whose interstices are 4–6 times their width. Microsculpture of very fine radial riblets, 6–12 between each pair of major ribs, crossed by barely visible spiral riblets. Secondary spiral cording prominent and relatively crowded. Sutures impressed, whorls strongly rounded above, slightly flattened laterally above periphery and on basal margin. Color light yellow-horn, with broad, irregular, reddish flammulations that fade out on shell base. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 4.00 times in the diameter. Aperture subcircular, slightly flattened laterally above periphery, inclined about 20° from shell axis. Height of holotype 1.45 mm., diameter 2.43 mm.

**Holotype.**—Tonga: Vava'u, Station T-9, Mo'ungalafa, near Tu'anuku, about 14 miles southwest of Neiafu, at 700 ft. elevation. Collected dead in leaf mould from patches of heavy forest by Laurie Price on January 3, 1966. FMNH 158449.

**Range.**—Southern part of Vava'u, Tonga Islands.

**Paratypes.**—Vava'u: near Toulou (Station T-8), 2 miles south of Neiafu in leaf mould in coral rubble under trees above strandline (16 specimens, FMNH 152488); Mo'ungalafa, near Tu'anuku (Station T-9), about 14 miles southwest of Neiafu in leaf mould from heavy forest at 700 ft. elevation (69 specimens, FMNH 152414); Muietola, 15 miles west of Neiafu (Station T-10) at 400 ft. elevation in heavy forest (3 specimens, FMNH 158455); cliffs at end of peninsula past Makave Village (Station T-12), 2½ miles southeast of Neiafu at 200 ft. elevation from leaf mould (1 specimen, FMNH 152360).

**Remarks.**—The four localities for *Sinployea vicaria paucicosta* are all on the south and southeast coasts of Vava'u. Material of the nominate race is known on Vava'u from the original collection of Graeffe in the 1860s, 265 shells from near Holonga (Station T-13) on the north tip, and four juvenile specimens from the north side (BPBM 87860) collected at 200–350 ft. elevation by J. E. Hoffmeister on July 10, 1928. It is probable that they are geographic races, but the possibility does exist that the variation is ecophenotypic or that they are separate species. Unfortunately, weather conditions were so dry that no living material could be obtained of *S. v. paucicosta* (see also p. 183).

Material from Stations T-8 and T-9 differs slightly in size (table XXVIII) but is almost identical in proportions and ribbing. Three examples from Station T-10 are subadult. The single shell from Station T-12 is badly worn and quite large, diameter 3.13 mm. One portion of the shell contains traces of widely spaced ribbing in the suture. Although it has been referred to this subspecies, the measurements have not been used in figuring means and ranges because it might belong to the nominate race. Further collecting is needed in order to establish the identity of this population.

The name *paucicosta* refers to the reduced number of major radial ribs that characterize this taxon.

***Sinployea rotumana* (E. A. Smith, 1897). Figure 61d–f.**

*Charopa rotumana* E. A. Smith, 1897, Ann. Mag. Nat. Hist., (6) 20, p. 520—Rotuma Island; Hedley, 1899, Mem. Australian Mus., 3 (7), p. 488—as a synonym of "*Charopa modicella*" (= *Sinployea ellicensis*) from Funafuti.

**Diagnosis.**—Shell of average size, diameter 2.60–3.24 mm. (mean 2.84 mm.) with 4–4½ normally coiled whorls. Apex and spire slightly to moderately and evenly elevated, last whorl descending more rapidly, spire protrusion about ⅓–¼ body whorl width, H/D ratio 0.481–0.607 (mean 0.547). Apical sculpture of 8–11 (mean 9.67) fine spiral cords. Postnuclear sculpture of low, rounded, rather crowded, strongly protractively sinuated radial ribs, 84–144 (mean 105.2) on the body whorl, whose interstices are 1½–3 times their width. Ribs/mm. 9.79–14.15 (mean 11.74). Microsculpture of fine ra-

dial riblets, 4–7 between each pair of major ribs, slightly finer and more crowded spiral riblets, with secondary spiral cording that becomes extremely fine on lower spire and very crowded. Umbilicus open, U-shaped, last whorl decoiling slightly more rapidly, contained 3.93–4.86 times (mean 4.32) in the diameter, margins rounded. Sutures deep, whorls rounded to strongly compressed laterally above periphery, aperture inclined about 20° from shell axis.

*Sinployea rotumana* (fig. 61d–f) has the major ribbing lower and less prominent, the secondary spiral cording much more crowded, and the body whorl more strongly flattened laterally than in *S. vicaria* (fig. 58a–c). *Sinployea atiensis* (fig. 44d–f) from the Cook Islands has fewer major radial ribs, more apical cords, and much more widely spaced secondary spiral cording. There are also subtle differences in umbilical and whorl contours.

**Description.**—Shell of average size, with a little more than 4 normally coiled whorls. Apex and early spire barely elevated, body

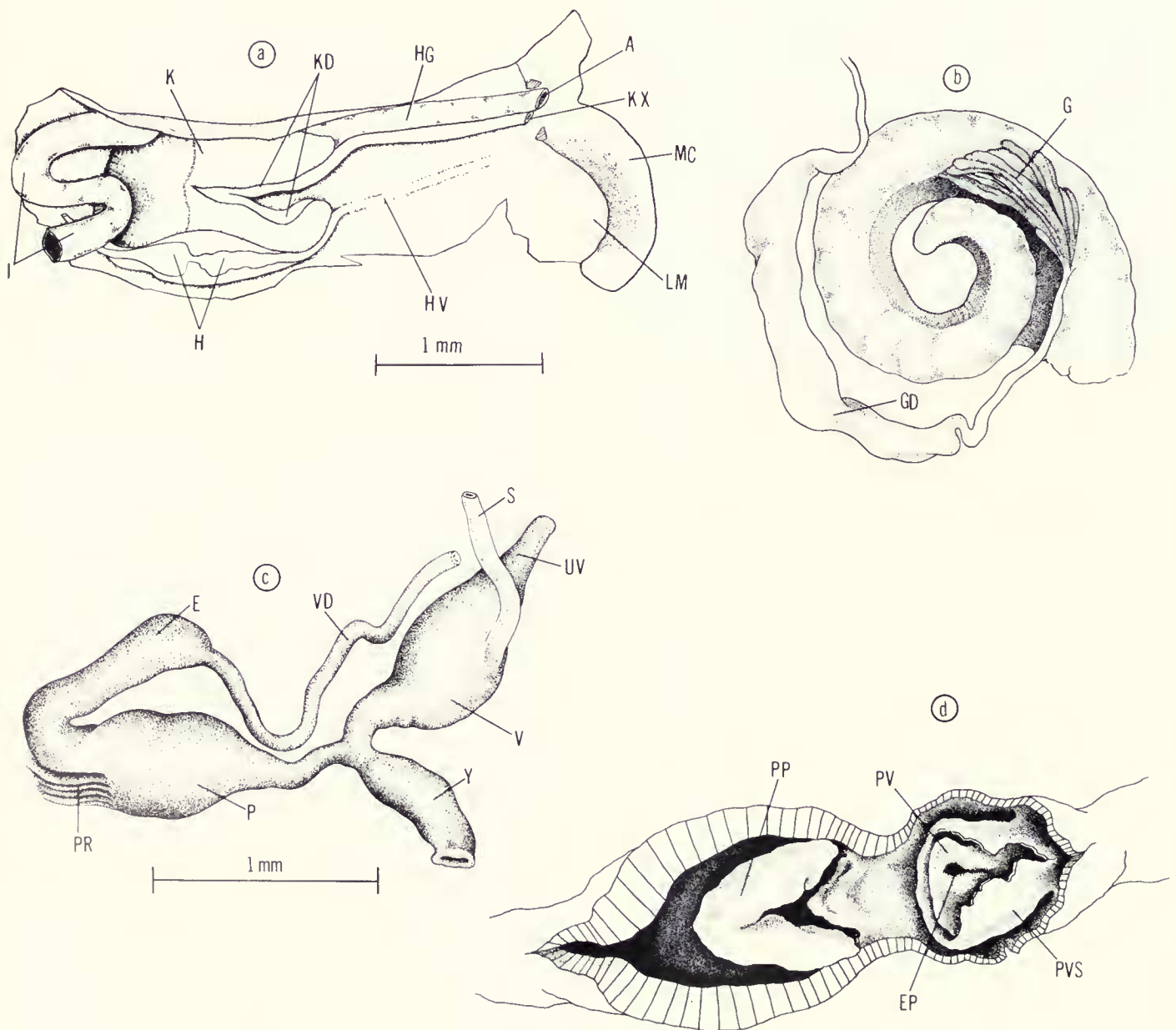


FIG. 60. Anatomy of the Tongan *Sinployea vicaria vicaria* (Mousson). Station T-13, near Holonga, Vava'u, Tonga Islands. FMNH 152373: a, pallial region; b, apical genitalia; c, terminal genitalia; d, interior of penis. Scale lines equal 1 mm. (CW).



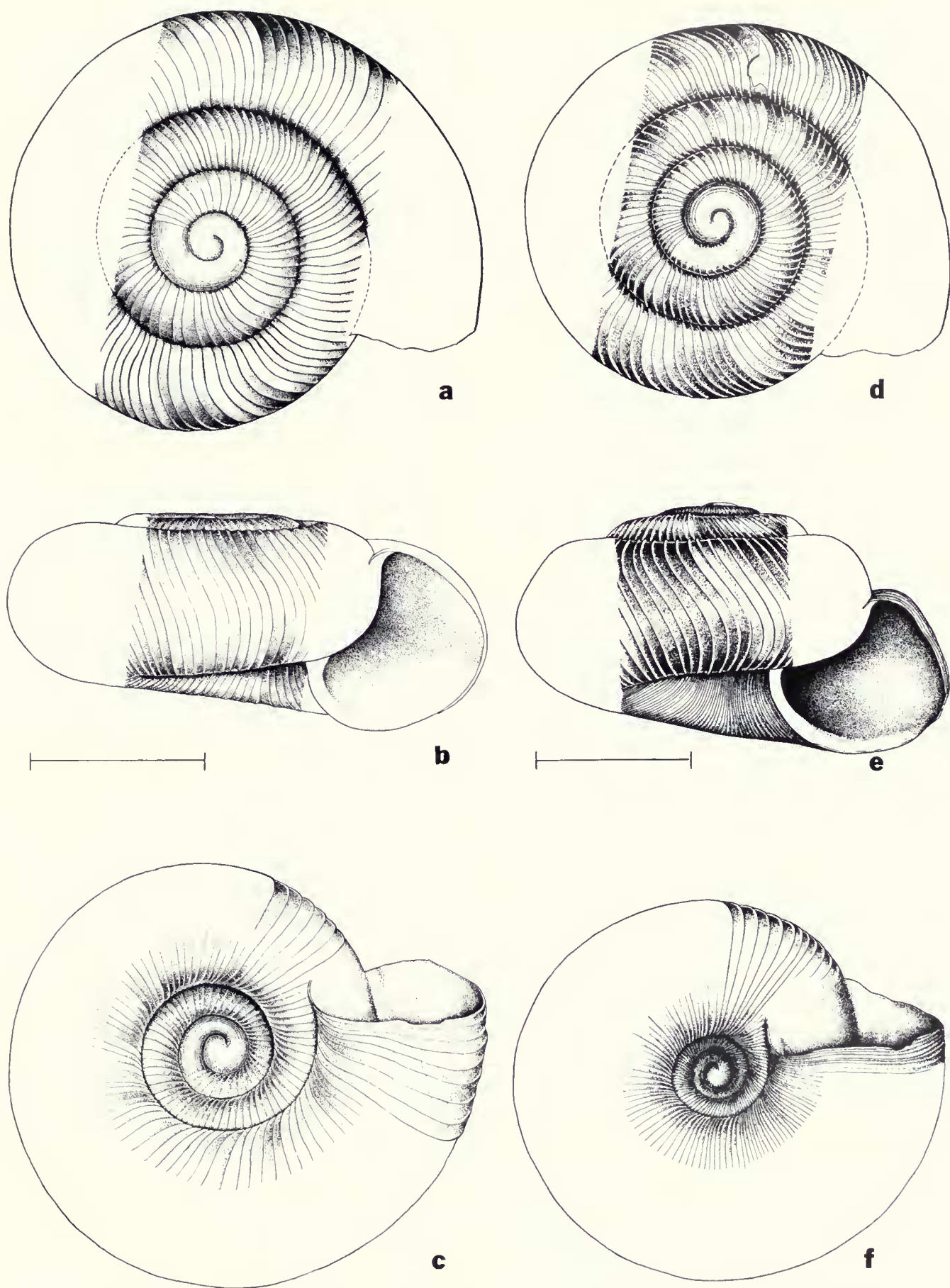


FIG. 61. **a-c**, *Sinployea pseudovicaria*, new species. Vaitupu, Ellice Islands. Holotype. BPBM 189682; **d-f**, *Sinployea rotumana* (E. A. Smith). Rotuma Island. BPBM 187049. Scale lines equal 1 mm. (SH).

whorl descending a little more rapidly, H/D ratio 0.497. Apical whorls 1%, sculpture of 10 prominent spiral cords, with a very faint secondary sculpture of radial riblets on last quarter whorl. Postnuclear whorls with prominent, rounded, low, slightly protractively sinuated radial ribs, 87 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets crossed by exceedingly fine spiral riblets with a secondary sculpture of minor, very crowded spiral cords. Sutures deep, whorls strongly rounded above, almost evenly rounded on outer and basal margins. Color light yellowish horn with broad, irregular reddish flammulations coalescing on base of shell. Umbilicus narrow, U-shaped, regularly decoiling, contained 4.22 times in the diameter. Aperture subcircular, slightly flattened laterally above periphery, inclined about 20° from the shell axis. Height of lectotype 1.38 mm., diameter 2.78 mm.

*Lectotype*.—Rotuma Island. Collected by J. Stanley Gardiner. BMNH 77.11.8.57.

*Range*.—Rotuma Island, 300 miles northwest of Fiji.

*Paratypes*.—BMNH 77.11.8.58–63.

*Material*.—Rotuma (1 specimen, BPBM 187049).

*Remarks*.—The single specimen collected by Harold St. John in 1938 (BPBM 187049) has the body whorl more compressed laterally above the periphery, but otherwise compares well with the type set. Differences from *Sinployea vicaria* and *S. atiensis* are covered in the diagnosis above.

### *Sinployea ellicensis*, new species.

Materials from Funafuti and Nukulaelae collected by Graeffe in 1868 and Charles Hedley in 1899 differ from the Tongan *S. vicaria* (fig. 58a–d) in their stronger ribbing and nearly circular aperture. Species of similar size from Eastern Polynesia have the aperture strongly flattened laterally above the periphery and usually show large differences in sculpture and/or shape. Species from Fiji, such as *S. godeffroyana* (fig. 69a–c) and *S. princei* (fig. 65a–c), differ in ribbing and higher spire (latter) or umbilical shape and much finer ribbing (former).

Recognition of two subspecies is done with some hesitation because only a single collection has been made on Nukulaelae. Specimens from this island are much smaller and have more apical cords than the examples from Funafuti. Although an equally great size difference is found between populations of *Sinployea vicaria* on Tongatapu and Eua Islands (table XXVIII), the distinct difference in island topography between the latter islands suggests that the distinctions may be environmentally correlated. Both Funafuti and Nukulaelae are atolls. Presumably there is no major habitat difference involved.

### *Sinployea ellicensis ellicensis*, new species and subspecies. Figure 62a–c.

*Patula vicaria* Mousson, 1873 (not Mousson, 1871), J. de Conchyl., 21, p. 104—Funafuti, Ellice Islands.

*Charopa modicella* Hedley, 1899 (not Férussac, 1840), Mem. Australian Mus., 3 (7), p. 488—Funafuti, Ellice Islands.

*Diagnosis*.—Shell small, diameter 2.20–2.81 mm. (mean 2.47 mm.), with 4–4½ rather tightly coiled whorls. Apex and spire slightly to moderately and evenly elevated, body whorl descending

more rapidly, spire protrusion about ¼–½ body whorl width, H/D ratio 0.496–0.561 (mean 0.549). Apical sculpture of 8–12 (mean 9.42) prominent spiral cords. Postnuclear whorls with prominent, rounded, crowded, slightly protractively sinuated radial ribs, 79–125 (mean 100.3) on the body whorl, whose interstices are usually less than twice their width. Ribs/mm. 10.55–16.69 (mean 13.23). Microsculpture of fine radial riblets, 3–5 between each pair of major ribs, barely visible and extremely crowded spiral riblets, with a secondary microsculpture of spiral cords slightly larger and more widely spaced than the microradials. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.48–5.46 times (mean 4.39) in the diameter, margins rounded. Whorls strongly and evenly rounded, aperture circular, not or only slightly flattened laterally above periphery, inclined about 20° from shell axis.

*Sinployea ellicensis* (fig. 62a–c) differs from the Tongan *S. vicaria* (fig. 58a–c) in its smaller size, lower spire protrusion, larger radial ribs, and more rounded whorl contours. *Sinployea ellicensis nukulaelaeana* (fig. 62d–f) is much smaller and has more apical cords. *Sinployea princei* (fig. 65a–c) has more whorls, monochromatic coloration, and only traces of secondary spiral cording.

*Description*.—Shell smaller than average, with 4½ normally coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending much more rapidly, H/D ratio 0.556. Apical whorls 1%, sculpture of 10 prominent, relatively widely spaced spiral cords. Postnuclear whorls with rounded, relatively crowded, protractively sinuated radial ribs, 119 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets, 3–6 between each pair of major ribs, crossed by barely visible spiral riblets and rather crowded secondary spiral cords. Sutures deeply impressed, whorls strongly rounded above, very slightly flattened laterally above periphery. Umbilicus narrowly U-shaped, last whorl decoiling more rapidly, contained 3.89 times in the diameter. Color light yellowish horn with vague, irregular reddish flammulations, fainter on base of shell. Aperture circular, slightly flattened laterally above periphery, inclined about 10° from the shell axis. Height of holotype 1.56 mm., diameter 2.81 mm.

*Holotype*.—Ellice Islands: Funafuti. Collected by Charles Hedley. AMS C.6124.

*Range*.—Funafuti, Ellice Islands.

*Paratypes*.—Ellice Islands (3 specimens, ex BPBM 1667): Funafuti (102 specimens, AMS C.6124, Zurich, DMW MF-8810, FMNH 116981, FMNH 158451).

*Remarks*.—Adult specimens in the Mousson collection are distinctly higher and slightly larger (table XXIX) than those collected by Hedley (AMS C.6124). Probably this is another example of collection bias toward retention of larger individuals. Differences from *Sinployea vicaria* are covered in the diagnosis above. Although direct comparison of examples leaves no doubt that they are distinct, measurements do overlap extensively. Unlocalized specimens would be hard to identify without direct comparisons. Measurements of *S. princei* (Liardet) are almost identical (table XXX), but there is a distinct difference in coiling pattern.

### *Sinployea ellicensis nukulaelaeana*, new subspecies. Figure 62d–f.

*Diagnosis*.—Shell very small, diameter 1.99–2.20 mm. (mean 2.08 mm.), with 3½–4 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.496–0.561 (mean 0.533). Apical sculpture of 11–13 (mean 11.67) prominent spi-



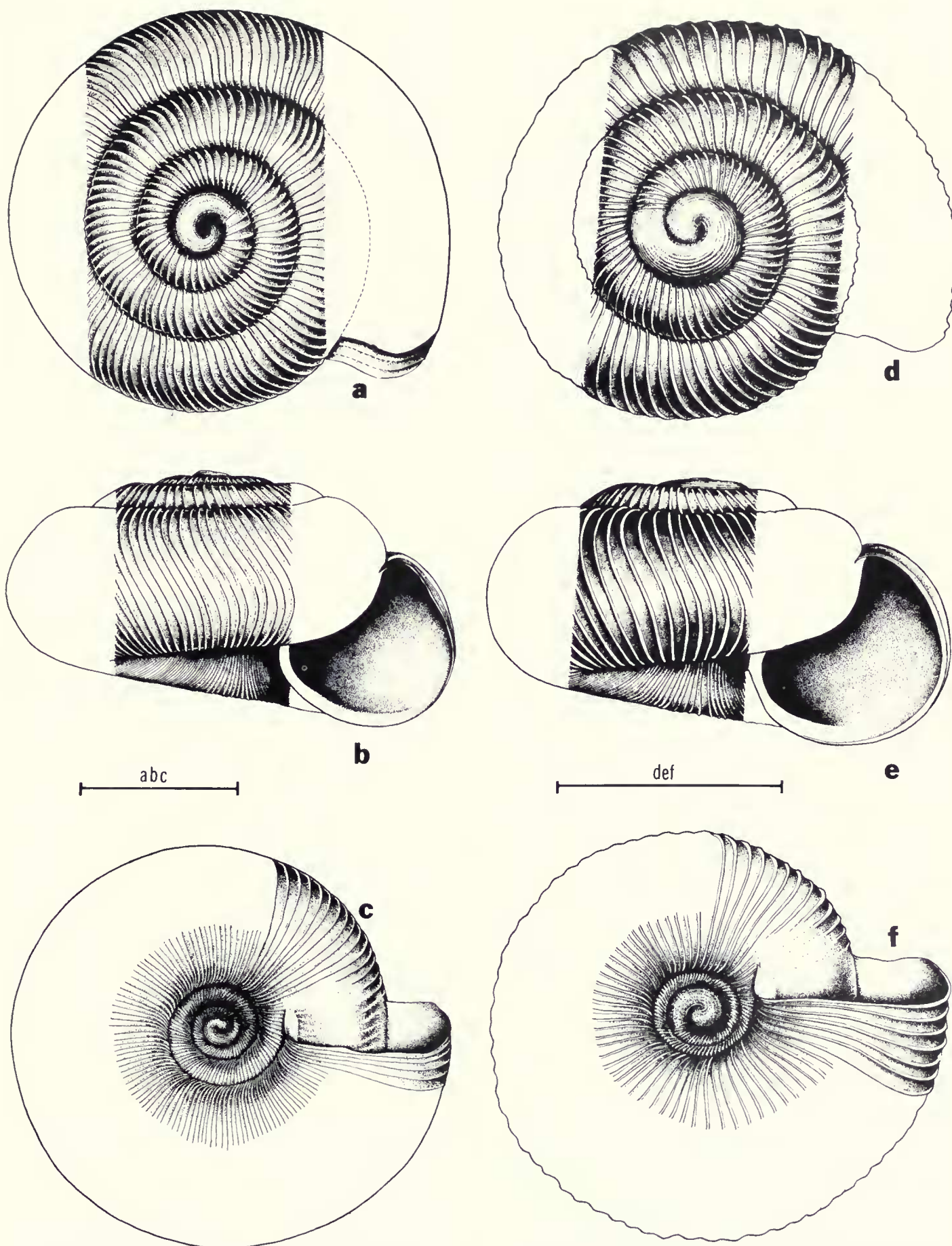


FIG. 62. a–c, *Sinployea ellicensis ellicensis*, new species and subspecies. Funafuti, Ellice Islands. Holotype. AMS C6124; d–f, *Sinployea ellicensis nukulaelaeana*, new subspecies. Nukulaelae, Ellice Islands. Holotype. AMS C6123. Scale lines equal 1 mm. (SH).

TABLE XXIX. - LOCAL VARIATION IN WESTERN POLYNESIAN SINPLOYEA.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>ellicensis</u>						
<u>ellicensis</u>						
Zurich	10	104.1±3.16 (91-125)	13.38±0.474 (11.02-16.71)	1.42±0.023 (1.29-1.51)	2.50±0.028 (2.40-2.65)	0.570±0.0066 (0.534-0.596)
AMS C6124	21	98.1±2.33 (79-119)	13.23±0.238 (10.55-16.69)	1.29±0.022 (1.14-1.57)	2.42±0.033 (2.22-2.83)	0.533±0.0061 (0.486-0.592)
<u>ellicensis</u>						
<u>nukulaelaeana</u>						
AMS C6123	6	84.5±4.85 (72-102)	13.02±0.734 (11.08-15.20)	1.11±0.016 (1.06-1.16)	2.08±0.032 (1.99-2.20)	0.533±0.0102 (0.496-0.561)
<u>pseudovicaria</u>						
Vaitupu BPBM 1667	5	113.5±4.51 (109-118)	11.15±0.156 (10.99-11.30)	1.55±0.066 (1.42-1.76)	3.18±0.050 (3.05-3.34)	0.487±0.0152 (0.454-0.525)
Zurich	3	111.3±4.34 (107-120)	10.81±0.020 (10.79-10.85)	1.58±0.029 (1.52-1.62)	3.30±0.121 (3.18-3.54)	0.479±0.0121 (0.458-0.500)
Eua BPBM 7983	2	87.0±6.02 (81-93)	8.54±0.110 (8.43-8.65)	1.53±0.082 (1.45-1.61)	3.24±0.181 (3.06-3.42)	0.472±0.0001 (0.471-0.473)
Zurich	3	100.0±7.51 (87-113)	9.19±0.371 (8.50-9.77)	1.67±0.048 (1.58-1.74)	3.45±0.125 (3.26-3.68)	0.483±0.0157 (0.455-0.509)
<u>rotumana</u>						
BMNH 77.11.8.57-63	8	104.0±7.01 (84-144)	11.74±0.519 (9.79-14.15)	1.56±0.063 (1.26-1.82)	2.86±0.066 (2.62-3.26)	0.544±0.0138 (0.481-0.607)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	
<u>e.ellicensis</u>						
Zurich	4	3/8-(4 1/4-4 1/2)	0.59±0.022 (0.49-0.76)	4.24±0.117 (3.48-4.86)	10.5±0.77 (9-12)	
AMS C6124	4	1/8+(4-4 1/2)	0.55±0.016 (0.43-0.72)	4.43±0.081 (3.77-5.46)	9.42±0.21 (8-11)	
<u>e.nukulaelae.</u>						
AMS C6123	3	7/8-(3 5/8-4)	0.48±0.013 (0.44-0.53)	4.31±0.086 (4.13-4.66)	11.7±0.34 (11-13)	
<u>pseudovicaria</u>						
Vaitupu BPBM 1667	4	3/8(4 1/4-4 1/2)	0.95±0.044 (0.79-1.05)	3.35±0.197 (2.94-4.05)	11.7±0.33 (11-12)	
Zurich	4	1/2+(4 1/2-4 5/8)	1.12±0.050 (1.05-1.22)	2.93±0.034 (2.89-3.00)	11	
Eua BPBM 7983	4	3/8(4 1/4-4 1/2)	1.05±0.066 (0.99-1.12)	3.08±0.020 (3.06-3.10)	-----	
Zurich	4	1/2+(4 1/2-4 3/4)	1.10±0.079 (0.99-1.25)	3.17±0.109 (2.95-3.30)	9.5±0.50 (9-10)	
<u>rotumana</u>						
BMNH	4	1/4-(4-4 5/8)	0.65±0.025 (0.58-0.81)	4.35±0.117 (3.93-4.86)	9.67±0.88 (8-11)	

ral cords. Postnuclear sculpture of narrow, prominent, crowded, protractively sinuated radial ribs, 75-102 (mean 84.5) on the body whorl, whose interstices are 1½-3 times their width, often with periostracal extensions. Ribs/mm. 11.06-15.20 (mean 13.02). Microsculpture of fine radial riblets, 3-6 between each pair of major ribs, crossed by barely visible spiral riblets, with secondary spiral cording that is rather crowded and equal in spacing to microradials. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 4.13-4.66 times (mean 4.31) in the diameter, margins rounded. Aperture and whorls circular, slightly compressed laterally above periphery.

*Sinployea ellicensis nukulaelaeana* differs from the nominate race in possessing more apical spiral cords and in being much smaller.

*Description.*—Shell very small, with slightly less than 4 normally coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending rapidly, H/D ratio 0.547. Apical whorls 1½, sculpture of 12 prominent spiral cords. Postnuclear whorls with prominent, narrow, protractively sinuated, crowded, radial ribs, 72 on the body whorl, whose interstices are 1½-3 times their width. Microsculpture of fine radial riblets, 3-6 between each pair of major



ribs, barely visible spiral riblets, with relatively prominent and crowded secondary spiral cording. Sutures deep, whorls strongly rounded above, very slightly compressed laterally above periphery and on basal margin, with evenly rounded outer margin. Color light yellow-horn, with vague and irregular reddish flammulations that tend to coalesce on shell base. Umbilicus open, U-shaped, last whorl decoiling slightly more rapidly, contained 4.66 times in the diameter, margins rounded. Aperture circular, slightly flattened laterally above periphery and on basal margin, inclined about 15° from shell axis. Height of holotype 1.14 mm., diameter 2.07 mm.

*Holotype*.—Ellice Islands: Nukulaelae. AMS C.6123.

*Range*.—Nukulaelae, Ellice Islands.

*Paratypes*.—Nukulaelae (7 specimens, AMS C.6123, FMNH 158452).

*Remarks*.—Size differences between the races of *Sinployea ellicensis* (table XXIX) equal those found between the Tongatapu and Eua Island *S. vicaria* collected in 1965 (table XXVIII). Subspecific recognition in this case is based on the difference in apical cord count and absence of major topographic differences between Funafuti and Nukulaelae. There are no consistent sculptural or shape differences between the populations.

#### *Sinployea pseudovicaria*, new species. Figure 61a–c.

*Patula vicaria* var. *major* Schmeltz, 1869, Cat. Mus. Godeffroy, 4, p. 72—Vaitupu, Ellice Islands (nude name); Schmeltz, 1874, Cat. Mus. Godeffroy, 5, p. 93 (nude name).

*Patula modicella* Mousson, 1873 (not Férussac, 1840), J. de Conchyl., 21, pp. 104–105—Vaitupu, Ellice Islands.

*Diagnosis*.—Shell relatively large, diameter 3.03–3.52 mm. (mean 3.24 mm.), with 4¼–4% normally coiled whorls. Apex and early spire flat, lower spire descending slightly, body whorl descending moderately, spire protrusion about ⅓ body whorl width, H/D ratio 0.454–0.525 (mean 0.486). Apical sculpture of 10–13 (mean 11.75) fine spiral cords. Postnuclear whorls with fine, prominent, protractively sinuated radial ribs, 82–127 (mean 108.1) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 9.56–15.15 (mean 11.33). Microsculpture of prominent radial riblets, 3–6 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. No secondary spiral cording present. Umbilicus broadly open, regularly decoiling, cup-shaped, contained 2.89–4.05 times (mean 3.17) in the diameter, margins rounded. Whorls with subcircular outline, very slightly flattened laterally above periphery, inclined about 25° from shell axis.

The flat spire, widely open umbilicus, and larger size immediately separate *Sinployea pseudovicaria* from the other Ellice and Tongan species. *Sinployea lamellicosta* (fig. 40a–c) from Tahiti has an equally wide umbilicus and is nearly identical in size and proportions, but has comparatively few radial ribs, a depressed or flat spire, and fewer, more loosely coiled whorls.

*Description*.—Shell rather small, with 4¼ relatively loosely coiled whorls. Apex and early spire flat, last whorl barely descending, H/D ratio 0.458. Apical whorls 1%, sculpture of 13 moderately prominent spiral cords. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, 82 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of fine, crowded radial riblets with much finer and more crowded spiral riblets. Sutures deeply impressed, whorls slightly shouldered above, body whorl slightly flattened laterally above periphery. Color partially leached from shell with dark, reddish brown flammulations remaining. Umbilicus broadly open, U-shaped, regularly decoiling,

contained 2.76 times in the diameter. Aperture circular, slightly flattened above periphery, inclined about 25° from shell axis. Height of holotype 1.25 mm., diameter 2.73 mm.

*Holotype*.—Ellice Islands: Vaitupu. Collected by L. Isaacs in May, 1941. BPBM 189682.

*Range*.—Vaitupu, Ellice Islands.

*Paratypes*.—Ellice Islands (5 specimens, BPBM 1667); Vaitupu (8 specimens, BPBM 106246, BPBM 189682, Zurich, FMNH 158450).

*Material*.—“Eua” (error) (7 specimens, BPBM 7983 ex Mus. Godeffroy, FMNH 116980, Zurich ex Mus. Godeffroy).

*Remarks*.—Although the holotype is subadult, it comes from the only set whose locality data can be accepted without question. The specimens from the Museum Godeffroy labeled “Eua” are essentially identical to the Vaitupu shells (table XXIX) and probably were accidentally mislabeled. Nothing at all similar has been recorded from Eua subsequently.

In view of the confusion between this species and *vicaria* in the older literature, I have chosen to use the name *pseudovicaria*.

#### *Sinployea kusaieana*, new species. Figures 63a–c, 67h.

*Diagnosis*.—Shell smaller than average, diameter 2.52–2.75 mm. (mean 2.60 mm.) with 3¼–4% normally coiled whorls. Apex and spire almost flat, slightly and evenly to moderately elevated, last whorl descending somewhat to much more rapidly, spire protrusion about ½ body whorl width, H/D ratio 0.462–0.542 (mean 0.506). Apical sculpture of 8–10 (mean 9.20) fine, rather inconspicuous spiral cords, whose interstices are 3–4 times their width. Postnuclear sculpture of prominent, strongly protractively sinuated, rather crowded, V-shaped radial ribs, 84–103 (mean 91.1) on the body whorl, whose interstices are 3–5 times their width. Microsculpture of very fine radial riblets, 5–10 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, with secondary spiral cording slightly more prominent than microradials, whose interstices are about 3 times their width. Umbilicus broadly open, V-shaped, last whorl usually decoiling more rapidly, contained 3.21–3.67 times (mean 3.51) in the diameter, margins rounded. Suture deep, whorls strongly rounded above, flattened laterally above periphery and weakly flattened in columellar margin. Aperture subcircular, flattened laterally above periphery, inclined about 20° from shell axis. Color reddish yellow-horn, without darker markings.

*Sinployea kusaieana* (fig. 63a–c) differs from the other barrier-free Caroline Island species by its possession of an epiphallus, vergic papilla, and *Sinployea*-type stimulatory pad in the penis, plus having the kidney arms equal in length. *Trukcharopa trukana* (fig. 63d–f) is dark reddish brown in color and has an average of 150 major ribs on the body whorl but is virtually identical in many measurements (pp. 209–210). *Russatus nigrescens* (fig. 89d–f) is much more loosely coiled and very much larger in size with fewer whorls and a very narrow umbilicus. *Kubaryiellus kubaryi* (fig. 89a–c) has a depressed apex and is much larger. The most similar Polynesian species are *S. navutuensis* (fig. 68d–f) from the Lau Archipelago, which has 127–147 ribs on the body whorl and averages one-quarter whorl less, and *S. rotumana* (fig. 61d–f) and *S. vicaria* (fig.

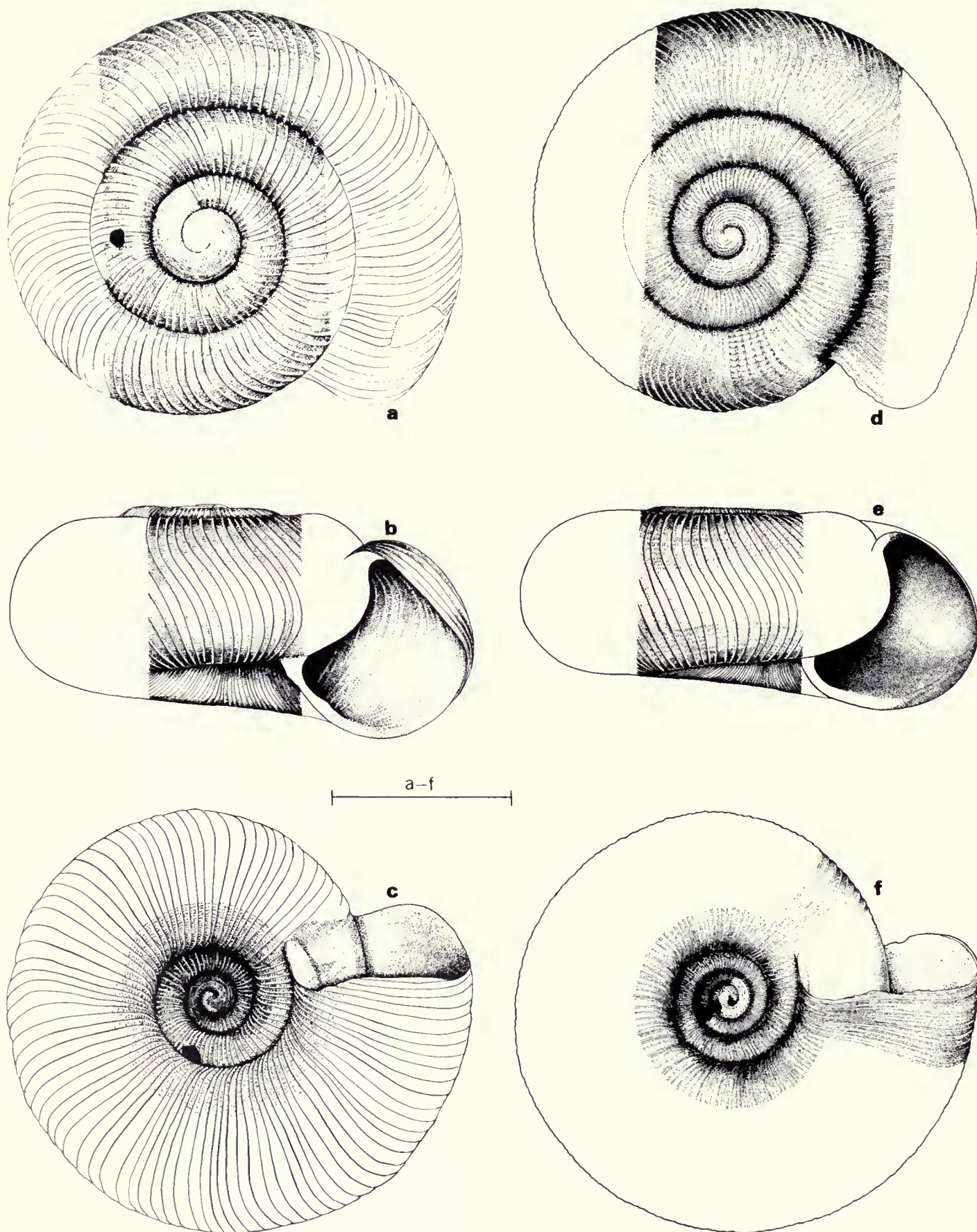


Fig. 63. a–c, *Sinployea kusaieana*, new species. Station 44, Lele Islet, Kusaie, Caroline Islands. Holotype. BPBM 155874; d–f, *Trukcharopa trukana*, new species. Station A5, Mt. Urupot, Tol Islet, Truk, Caroline Islands. Holotype. BPBM 189318. Scale line equals 1 mm. (a–c, e, SH; d, f, MM).



58a-c), which have higher spires and narrower umbilici.

*Description*.—Shell smaller than average, with 4 moderately tightly coiled whorls. Apex flat, spire and body whorl descending slightly, H/D ratio 0.481. Embryonic whorls  $1\frac{1}{2}$ , sculpture of 9 narrow, relatively low spiral ribs. Remaining whorls with sculpture of crowded, rounded, protractively sinuated radial ribs, 84 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets, 5–10 between each pair of major ribs, crossed by finer, slightly more crowded spiral ribs, with more prominent, rounded, more widely spaced spiral cords. Sutures deeply impressed, whorls sharply rounded above, somewhat flattened laterally with slightly flattened columellar margin. Umbilicus broadly V-shaped, regularly decoliling, contained 3.44 times in the diameter. Color light reddish yellow-horn without traces of flammulations. Aperture subcircular, strongly flattened laterally above periphery with slightly flattened columellar margin, inclined about  $15^\circ$  from the shell axis. Height of holotype 1.25 mm., diameter 2.60 mm.

*Holotype*.—Caroline Islands: Kusaie, Station 44, Lele Islet, under stones and logs at 3 ft. elevation. Collected by S. Ito and Yoshio Kondo on January 21, 1936. BPBM 155874.

*Range*.—Kusaie, Caroline Islands.

*Paratypes*.—Kusaie: Lele Islet (Station 44) under stones and logs at 3 ft. elevation (59 specimens, BPBM 155874-7); Mot District (Station 66) 300 yd. west of Kefwas, 10 yd. inland at 4–5 ft. elevation (1 specimen, BPBM 156179).

*Remarks*.—Both of the known localities on Kusaie are lowland elevations under disturbed conditions. Quite possibly *Sinployea kusaieana* will be found to occur on other of the Eastern Caroline Islands.

*Description of soft parts*.—Foot and tail equal to shell diameter, tapering posteriorly. Sole and pedal grooves typical. Gonopore in normal position.

Body color light yellow-white, without darker markings.

Pallial region extending  $\frac{5}{8}$  whorl apically, without unusual features. Lung roof clear, no granulations. Kidney typically bilobed, maximum length 1.0–1.3 mm., lobes equal in length. Ureter typical, narrow strip of lung roof visible between arms.

Ovotestis, hermaphroditic duct, albumen gland, talon, prostate (fig. 67h, DG), and uterus typical, no unusual features.

Vas deferens (VD) not expanded in any area, entering epiphallus through usual pore. Epiphallus (E) about half as long as penis, slender, only weakly expanded. Penial retractor (PR) short, arising from diaphragm, inserting on head of penis lateral to epiphallic junction. Penis (P) about 1 mm. long, quite slender, upper half weakly expanded, internally with typical vergic papilla and small stimulatory pad. Atrium (Y) long and slender.

Free oviduct (UV) typical. Spermatheca (S) with basal portion of shaft less expanded than usual. Vagina (V) tapering to atrium.

(Based on BPBM 155874, 4 whole and several partial specimens.)

### *Sinployea* sp.

*Material*.—Marianas: Saipan, north edge of Garampan at base of a century plant (2 specimens, BPBM 190043).

*Remarks*.—The two dead, somewhat worn shells collected by Harold W. Harry in October 1944 are not referable to any described species. They are most similar to *Sinployea atiensis* (Pease) from the Cook Islands and *S. ellicensis* from Funafuti, but are smaller and

with fewer whorls than the former and higher and with fewer ribs than the latter. The coiling pattern is looser than in either species.

Because they were collected under an introduced plant in an urban area, the possibility exists that they were introduced on plants from Polynesia. Without additional information, I am not willing to accept this as a valid range extension and include the specimens here only to call attention to the need for making more collections in the Northern Marianas. Measurements of the shells have been included in Table XXVII for convenient reference.

### FIJIAN *Sinployea*

There is an extraordinary diversity of *Sinployea* and derivative genera in Fiji and the Lau Archipelago (table XXX). Two species, *S. irregularis* (Garrett) and *S. godeffroyana*, are known from Viti Levu; the former also lives on Ovalau; and one species, *S. princei* (Liardet), is known from Taveuni and possibly Kandavu. The absence of any records from relatively large islands such as Vanua Levu, Koro, Ngau, Moala, and Thithia probably are artifacts of collecting activity. I know of no significant collections of land mollusks from any of the above islands. Undoubtedly, most of them will be found to have *Sinployea* present. Six species of *Sinployea* are known from the Lau Group, one of them, *S. inermis* (Mousson), with three geographic races. Genera that are probably derived directly from *Sinployea* include *Maafu thaumasius*, which is restricted to Nayau in the Lau Group, and *Ba humbugi* on Viti Levu. The former agrees in shell microsculpture with *Sinployea inermis*, although radically altered in shell form and size (fig. 76a–c), whereas the latter (fig. 74a–c) can be derived without difficulty from *S. irregularis*. I am less certain of the probable derivation for the Vanua Mbalavu *Lauopa mbalavuana* (fig. 77a–c).

In Polynesia it is very unusual to have any sympatric occurrences of *Sinployea* or even for two species to live in the same valley, but there is extensive sympatry in the southern Lau Archipelago. The northern Lau islands of Kimbombo, Vanua Mbalavu, Munia, and Mango have only single species records, either *S. inermis* or *S. adposita*. On Nayau, *S. adposita* and *S. lauensis* were taken at the same station, whereas on Aiwa, Tuvutha, and Lakemba both *S. adposita* and *S. inermis* were found together. On Oneata, both *S. navutuensis* and *S. adposita* were collected, but not at the same stations. Wangava had large numbers of *S. recursa* and a few *S. lauensis* taken together, whereas on Navutu-i-Loma H. S. Ladd collected *S. inermis*, *S. lauensis*, and *S. navutuensis* together at two different stations. Finally, on Yangasa Levu large numbers of *S. inermis*, *S. adposita*, and *S. lauensis* were sympatric. Unfortunately most of these specimens were dead individuals collected during the July to August dry season. Soft parts were available only for *S. inermis* and *S. adposita*. Dissection of specimens from Station 97,

TABLE XXX. - RANGE OF VARIATION IN FIJIAN *SINPLOYEA*.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<i>angularis</i>	188	38.0(36-42)	5.67(5.28-6.16)	1.21(1.08-1.29)	2.11(2.02-2.27)	0.574(0.512-0.615)
<i>recursa</i>	108	R E D U C E D		1.66(1.51-1.84)	2.83(2.60-3.09)	0.587(0.562-0.634)
<i>princei</i> (Liardet)						
Taveuni	9	91.1(80-102)	12.06(11.84-13.80)	1.34(1.26-1.57)	2.43(2.35-2.68)	0.551(0.524-0.586)
Kandavu	4	96.3(84-119)	13.10(11.4-14.67)	1.27(1.17-1.45)	2.33(2.02-2.58)	0.545(0.521-0.577)
<i>inermis inermis</i> (Mousson)	197	80.9(65-104)	9.82(8.39-11.75)	1.46(1.18-1.84)	2.60(2.24-3.06)	0.562(0.500-0.629)
<i>inermis meridionalis</i>	169	72.2(53-104)	8.37(6.75-11.70)	1.64(1.32-1.94)	2.88(2.50-3.22)	0.566(0.505-0.655)
<i>inermis lakemba</i>	14	51.3(38-62)	7.01(4.67-8.20)	1.37(1.10-1.64)	2.36(2.14-2.86)	0.583(0.508-0.634)
<i>lauensis</i>	82	103.9(95-119)	11.53(10-93-14.46)	1.47(1.18-1.78)	2.76(2.40-3.13)	0.530(0.493-0.581)
<i>navutuensis</i>	29	136.7(121-147)	17.36(16.94-17.62)	1.32(1.16-1.49)	2.66(2.58-2.78)	0.498(0.499-0.566)
<i>adposita</i>	176	53.3(36-74)	5.28(3.35-7.23)	1.81(1.58-2.20)	3.29(2.70-3.62)	0.603(0.538-0.687)
<i>irregularis</i> (Carrett)	78	I R R E G U L A R		1.77(1.51-2.30)	2.87(2.50-3.52)	0.614(0.528-0.764)
<i>godeffroyana</i>	3	117.7(85-152)	28.36(20.99-38.03)	1.26(1.19-1.29)	2.12(1.95-2.32)	0.595(0.577-0.619)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW
<i>angul.</i>	3 7/8+(3 3/4-4)	0.35(0.23-0.40)	6.14(5.21-8.71)	14.6(13-16)	0.19(0.16-0.23)	0.62(0.59-0.66)	0.316(0.250-0.389)
<i>recur.</i>	3 7/8-(3 1/2-4 1/8)	0.43(0.33-0.53)	6.63(5.75-7.90)	15.9(14-18)	0.23(0.20-0.30)	0.86(0.81-0.91)	0.264(0.222-0.346)
<i>princ.</i> Tav.	3 3/4+(3 1/2-4 1/8)	0.57(0.49-0.63)	4.28(3.74-4.83)	9(8-10)	0.12(0.08-0.23)	0.81(0.70-0.89)	0.151(0.095-0.259)
Kan.	3 5/8+(3 1/2-4)	0.46(0.39-0.53)	4.76(4.14-5.19)	NOT AVAILABLE	0.13(0.10-0.18)	0.75(0.66-0.86)	0.179(0.130-0.250)
<i>i. ine.</i>	4-(3 1/2-4 5/8)	0.62(0.49-0.82)	4.17(3.47-4.69)	8.96(6-11)	0.16(0.10-0.25)	0.81(0.72-0.92)	9.192(0.115-0.280)
<i>i. mer.</i>	4 1/4+(3 7/8-4 5/8)	0.82(0.69-0.99)	3.51(3.07-3.81)	11.6(9-14)	0.20(0.13-0.26)	0.96(0.82-1.05)	0.207(0.140-0.285)
<i>i. lak.</i>	4+(3 3/4-4 1/2)	0.45(0.33-0.76)	5.54(3.78-7.10)	13.6(11-16)	0.19(0.13-0.23)	0.82(0.72-0.89)	0.226(0.153-0.259)
<i>lauen.</i>	3 7/8(3 1/2-4 1/4)	0.65(0.53-0.79)	4.24(3.88-4.65)	9.6(9-11)	0.10(0.03-0.16)	0.91(0.82-1.09)	0.113(0.038-0.161)
<i>navut.</i>	4 1/8(4-4 3/8)	0.78(0.76-0.82)	3.38(3.25-3.52)	10.3(9-11)	0.09(0.07-0.13)	0.74(0.66-0.79)	0.125(0.100-0.167)
<i>adpos.</i>	4 3/8+(4-4 7/8)	0.28(0.17-0.46)	11.9(7.85-17.0)	13.0(12-14)	0.24(0.13-0.33)	1.04(0.86-1.18)	0.227(0.133-0.275)
<i>irreg.</i>	3 3/4+(3 1/4-4 3/8)	0.64(0.39-0.92)	4.54(3.79-6.83)	13.5(16-20)	0.20(0.10-0.46)	0.96(0.86-1.09)	0.201(0.100-0.424)
<i>godef.</i>	3 3/4+(3 3/4-4)	0.42(0.33-0.56)	5.26(4.11-6.30)	9.7(8-11)	0.12	0.81	0.143

Toumba, Lakemba, Lau, showed that *S. adposita* had a longer penis with very small stimulatory pad and normal vergic papilla, whereas *S. inermis* had a shorter penis with very large stimulatory pad and small vergic papilla. On Viti Levu, *S. godeffroyana* and *S. irregularis* have been collected at the same station, and I have found *S. irregularis* and *Ba humbugi* under the same piece of bark.

Evidence from the white body color suggests that *S. irregularis*, *S. inermis*, and *S. adposita* are strictly terrestrial. Generally, semiarboreal species have gray color on the ommatophores and neck, sometimes also on the mantle collar edge. Two species, *S. angularis* and *S. recurva*, have greatly reduced sculpture, and I suspect that they may be semiarboreal or arboreal species. Unfortunately, they are known only from dead examples.

Patterns of distribution are relatively simple. *Sinployea irregularis* and *S. godeffroyana* are widely distributed on forested areas of Viti Levu. *Sinployea princei* was described from Taveuni, and essentially identical specimens coming from the Rolle collection are labeled Kandavu. *Sinployea inermis* and *S. adposita* are widely distributed in the Lau Archipelago, with the former having a slightly greater range. *Sinployea recurva* is known only from Wangava, and *S. angularis*, only from Namuka. *Sinployea navutuensis* is recorded from Navutu-i-Loma, and a single shell from Oneata has been referred here with some hesitation. *Sinployea lauensis* has a fairly wide range in southern Lau, having been found on Nayau, Wangava, Namuka, Navutu-i-Loma, and Yangasa Levu.

Many of the Lau Group have never been collected for land mollusks. Generally, only a single or at most



two stations made in a hurried visit of one to two days account for the collecting done to date on most islands. Obviously there are splendid opportunities for further field work. Particularly important will be efforts to work out patterns of species isolation between sympatric taxa.

*Sinployea inermis* (Mousson) from the Lau Archipelago, *S. princei* (Liardet) from Taveuni and Kandavu, and *S. irregularis* (Garrett) from Viti Levu are the generalized Fijian species. *Sinployea inermis* is one of the most "average" *Sinployea*, with the monochrome coloration, details of sculpture, and proportions (fig. 66a–c) differentiating it from the Tongan *S. vicaria* (Mousson) (fig. 58a–c) and the Ellice Island *S. ellicensis* (fig. 62a–c). Subspecies of *S. inermis* depart further from the typical pattern, but are still generalized in shape and form. *Sinployea princei* (fig. 65a–c) has a weakly flammulated color pattern, much more crowded radial ribbing, and reduced secondary spiral cording, but is very similar to *S. inermis*. Greater differences are shown by *S. irregularis* (fig. 65d–f). The spire is flat, sutures deep, apical sculpture much finer and more numerous, ribbing very irregular, body whorl often abruptly descending, and the size is slightly larger.

Several species show minor character changes. *Sinployea adposita* (Mousson) (fig. 69d–f) can be derived from *S. inermis* by increase in size, narrowing of the umbilicus, and increase in rib spacing. The two species are sympatric and show character displacement in penial structure, with *S. inermis* (fig. 67e–f) having the stimulatory pad and muscular collar proportionately larger than usual and the vergic papilla shorter, whereas in *S. adposita* (fig. 67g) the vergic papilla is quite large. *Sinployea lauensis* (fig. 68a–c) has more crowded ribbing, a less protruded spire, fatter body whorl, and more rapidly decoiling umbilicus. It has not been dissected. *Sinployea navutuensis* (fig. 68d–f) has much more crowded radial ribbing, a wider umbilicus, nearly flat apex, and lower H/D ratio. Two other Lau Archipelago species are more strongly differentiated. The slightly larger *S. recurva* (fig. 64a–c) has a strongly flammulated color pattern and the sculpture greatly reduced. No live material is known, but I suspect this may be a more arboreal species than most *Sinployea*. *Sinployea angularis* (fig. 64d–f) is reduced in size, has widely spaced radial ribbing, a narrow umbilicus, angulated periphery, and pale monochrome coloration. It has perhaps the most modified shell of any *Sinployea*. Possibly generic separation is warranted, but without study of the soft parts, I prefer a conservative treatment.

On Viti Levu, the monotypic genus *Ba* (p. 172) can be derived from *Sinployea irregularis* by a drastic change in coiling pattern, reduction in whorl count, closure of the umbilicus, and decrease in number of spiral apical cords. Anatomical changes are covered under the description of that species. The other Viti Levu species, *Sinployea godeffroyana* (fig. 69a–c), is

characterized by its small size, proportionately thick body whorl, and extremely crowded radial ribbing (mean ribs/mm. 28.4). It has not been dissected.

Undoubtedly there are additional species of *Sinployea* in both Fiji and the Lau Archipelago. Use of the following key can serve only as a general guide to affinities when more collections become available.

#### KEY TO THE FIJI AND LAU *Sinployea*

1. Main islands of Fiji .....2  
Lau Archipelago.....4
2. Ribbing irregular; apical cords more than 15; mean diameter more than 2.7 mm. ....*Sinployea irregularis* (Garrett, 1887)  
Ribbing regular; apical cord average 10; mean diameter less than 2.5 mm. ....3
3. Viti Levu; mean diameter about 2.1 mm.; ribs/mm. more than 20.....*Sinployea godeffroyana*, new species  
Taveuni and Kandavu; mean diameter about 2.3–2.4 mm.; ribs/mm. less than 15.....*Sinployea princei* (Liardet, 1876)
4. Mean diameter less than 3.0 mm.; mean D/U ratio less than 7 .....5  
Mean diameter more than 3.1 mm.; mean D/U ratio more than 10.....*Sinployea adposita* (Mousson, 1870)
5. Body whorl not angulated; mean diameter more than 2.3 mm. ....6  
Body whorl angulated; mean diameter about 2.1 mm.; Namuka.....*Sinployea angularis*, new species
6. Prominent major ribbing continuing to end of body whorl .....7  
Major radial ribbing widely spaced on spire, becoming reduced, then absent on body whorl.....*Sinployea recurva*, new species
7. Mean rib count 100–150 .....8  
Mean rib count 50–95 .....9
8. Mean D/U ratio less than 3.5; ribs/mm. more than 16; mean body whorl width about 0.75 mm. ....  
*Sinployea navutuensis*, new species  
Mean D/U ratio more than 4.0; ribs/mm. less than 15; mean body whorl width about 0.90 mm. ....  
*Sinployea lauensis*, new species
9. Mean D/U ratio usually much more than 3.8; Central and Northern Lau .....10  
Mean D/U ratio less than 3.6; Southern Lau .....  
*Sinployea inermis meridionalis*, new subspecies
10. Mean rib count less than 60; mean D/U ratio about 5.50; mean apical cords about 13; Lakemba .....  
*Sinployea inermis lakembana*, new subspecies  
Mean rib count more than 70; mean D/U ratio less than 4.50; mean apical cords about 9; Mango and Vanua Mbalavu.....*Sinployea inermis inermis* (Mousson, 1870)

#### *Sinployea angularis*, new species. Figure 64d–f.

**Diagnosis.**—Shell very small, diameter 2.02–2.27 mm. (mean 2.11 mm.), with 3¼–4 normally coiled whorls. Apex and spire moderately and usually evenly elevated, sometimes rounded above, body whorl descending a little more rapidly, spire protrusion almost ⅓ body whorl width, H/D ratio 0.512–0.615 (mean 0.574). Apical sculpture of 13–16 (mean 14.6) narrow and rather inconspicuous spiral cords. Postnuclear sculpture of low, rounded, widely spaced, strongly protractively sinuated radial ribs, 36–42 (mean 38.0) on the body whorl, whose interstices are 4–7 times their width. Ribs/mm. 5.28–6.16 (mean 5.67). Microsculpture of extremely fine radial riblets, more than 10 between each pair of major ribs, crossed by equally fine spiral riblets, with narrow, rather crowded secondary spiral cording, becoming broader and less distinct on body whorl. All microsculpture barely visible at 96× magnification. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 5.21–8.71 times (mean 6.14) in the diameter, margins rounded. Sutures impressed, whorls strongly rounded above, becoming strongly flattened laterally above obtusely angulated periphery, evenly rounded on

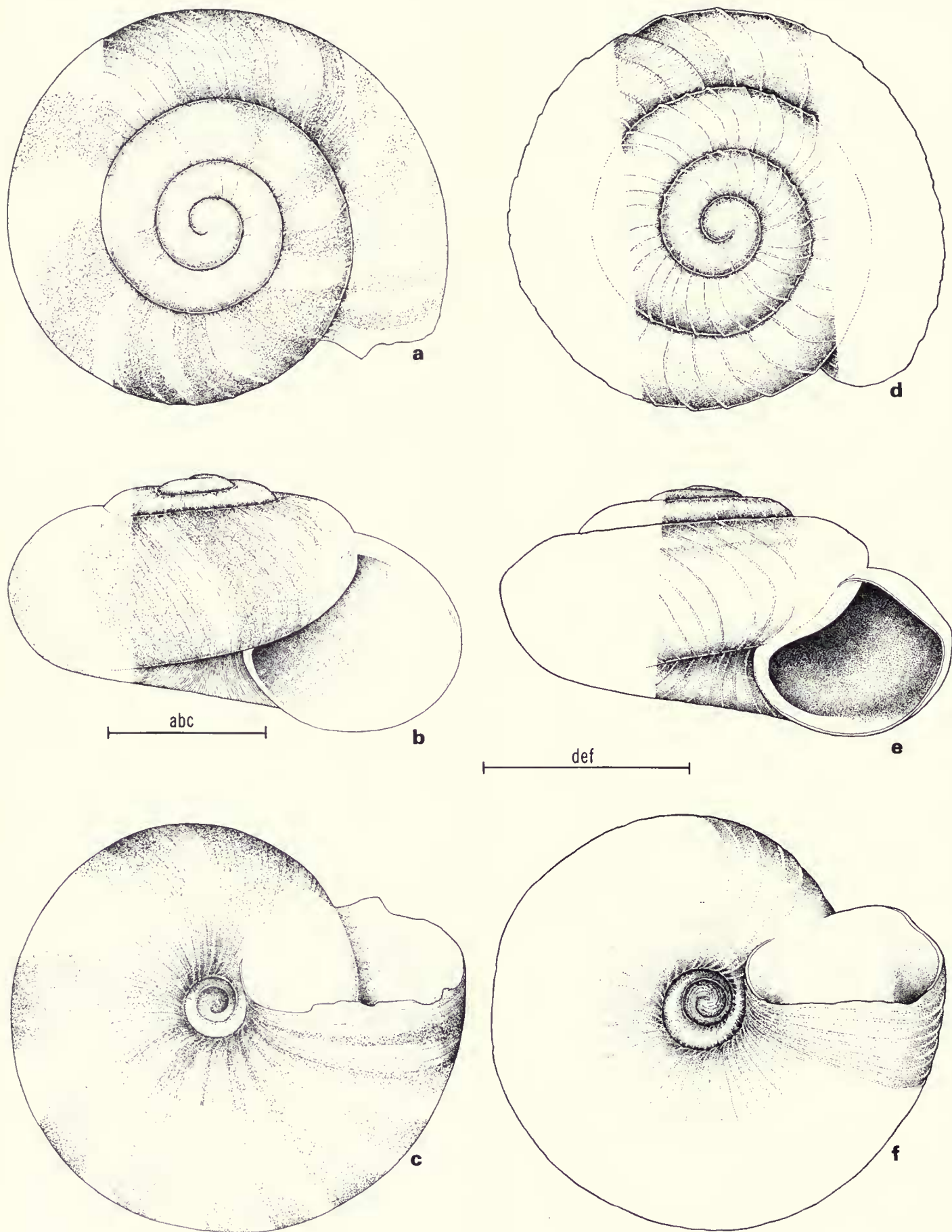


FIG. 64. a-c, *Sinployea recurva*, new species. Station 27, Wangava, Lau, Fiji. Holotype. BPBM 166967; d-f, *Sinployea angularis*, new species. Station 3, Namuka, Lau, Fiji. Holotype. BPBM 166616. Scale lines equal 1 mm. (MM).



outer and lower margins. Aperture inclined about 25° from shell axis.

Although both *Sinployea irregularis* from Viti Levu (fig. 65e) and *S. rudis* from Rarotonga (fig. 47e) give the appearance of having an angulated periphery because of supraperipheral flattening, only *S. angularis* (fig. 64e) of Polynesian-Fijian Charopidae has the periphery itself actually angulated. *Sinployea adposita* (fig. 69d-f) agrees in rib spacing, but is much, much larger and has a very narrow umbilicus. *Sinployea inermis* (fig. 66a-e) is much larger, with a less protruded spire, rounded periphery, and usually much more numerous and crowded ribbing.

**Description.**—Shell very small, with 4 moderately tightly coiled whorls. Apex and spire distinctly and evenly elevated, last part of body whorl slightly deflected below periphery of penultimate, H/D ratio 0.591. Embryonic whorls 1½, sculpture mainly eroded, with traces of fine spiral cords remaining. Postnuclear sculpture of low, rounded, protractively sinuated radial ribs, 36 on the body whorl, whose interstices are 4–7 times their width. Microsculpture of extremely fine radial riblets, crossed by much finer, more crowded spiral riblets and narrow, rather vague secondary spiral cords. Sutures relatively shallow on body whorl, slightly indented. Whorls with angulated periphery, somewhat flattened above and slightly flattened below with gently rounded basal margin. Umbilicus narrow, U-shaped, last whorl decoiling more rapidly, contained 5.50 times in the diameter. Color leached from shell. Aperture ovate with angulated periphery, inclined about 25° from the shell axis. Height of holotype 1.28 mm., diameter 2.17 mm.

**Holotype.**—Fiji: Lau Group, Namuka, Station 3, 500 ft. inland from Matandolo on north central part of island at 65–75 ft. elevation. Collected dead between rocks by H. S. Ladd on July 7, 1934. BPBM 166616.

**Range.**—Namuka, Lau Group, Fiji.

**Paratypes.**—Namuka: 500 ft. inland from Matandolo (Station 3) on north central part of island at 65–75 ft. elevation (187 specimens, BPBM 166616, BPBM 166642, BPBM 166669).

**Remarks.**—Only 14 (7.4%) of 188 *Sinployea angularis* were whole adults. The remainder were juveniles or badly broken specimens. Although an angulated periphery is extremely common in the Endodontidae and many of the New Caledonian and Austro-Zelandic endodontoid taxa, it is found otherwise among Pacific Island Charopidae only in the Marianas *Himeroconcha quadrasi* and *H. fusca* (fig. 105b, e). Hence the choice of *angularis* as specific name for this species.

Its elevated spire and angulated periphery separate it from any other Fijian species in appearance, but the pattern of sculpture is a modification of the same type seen in *S. inermis*. *Sinployea angularis* is much smaller than examples of *S. inermis*, coming closest in size to the Viti Levu *S. godeffroyana*. The latter has very numerous and crowded radial ribbing, plus the spire is much less protruded.

Possibly this is an arboreal species and should be generically separated from *Sinployea*. Without dissection and ecological data, I prefer to retain it in *Sinployea*. In size and shape it is the most drastically altered species.

### *Sinployea recurva*, new species. Figure 64a–c.

**Diagnosis.**—Shell of average size, diameter 2.60–3.09 mm. (mean 2.83 mm.), with 3½–4¼ normally coiled whorls. Apex and spire moderately to strongly elevated, body whorl descending more rapidly, spire protrusion more than ¼ body whorl width, H/D ratio 0.562–0.634 (mean 0.587). Apical sculpture of 14–18 (mean 15.9) fine spiral cords, often partly to completely eroded. Postnuclear sculpture of indistinct, low, broadly rounded, widely spaced radial ribs on the upper spire that become greatly reduced to absent by early part of body whorl. Vague traces of microreticulations on the upper spire become replaced by fine and crowded secondary spiral cords on body whorl. All microsculpture only visible under high magnification with oblique lighting. Umbilicus narrow, V-shaped, slightly and regularly decoiling, contained 5.75–7.90 times (mean 6.63) in the diameter, margins rounded. Sutures impressed, whorls strongly rounded above, compressed laterally above periphery, with slightly compressed basal margin. Color light yellow-horn, with irregular reddish flammulations that become narrower on shell base.

In spire elevation and general appearance, *Sinployea recurva* shows many similarities to *S. angularis*. The latter (fig. 64d–f) is much smaller, has an angulated periphery, and much more prominent radial ribbing. No other Polynesian or Micronesian Charopidae has the ribbing so greatly reduced, although this is frequent in New Caledonian, Australian, and New Zealand taxa and occurs sporadically in the Polynesian Endodontidae.

**Description.**—Shell of average size, with slightly less than 3¼ relatively loosely coiled whorls. Apex and spire evenly elevated, last whorl descending a little more rapidly, H/D ratio 0.582. Embryonic whorls 1¼, sculpture of about 15 fine spiral ribs, partially eroded. Postnuclear whorls with a few widely spaced, low, inconspicuous radial ribs on the upper spire, becoming reduced over most of the body whorl but reappearing on last quarter. Microsculpture of fine radial growth striae and very low, inconspicuous secondary spiral cording. Sutures relatively shallow, whorls gently rounded above, sloping flatly down to more strongly rounded periphery and slightly flattened basal lip, contained 7.82 times in the diameter. Color light yellowish white with vague irregular yellow-red or reddish brown flammulations. Aperture ovate, slightly flattened basally, inclined about 20° from the shell axis. Height of holotype 1.64 mm., diameter 2.83 mm.

**Holotype.**—Fiji: Lau Group, Wangava, Station 27, northeast end of island on an inland ridge, ¼ mile from shore, at 75 ft. elevation. Collected in soil under leaves and between rocks by H. S. Ladd on July 22, 1934. BPBM 166967.

**Range.**—Wangava, Lau Group, Fiji.

**Paratypes.**—Wangava: northeast end of island (Station 27), ¼ mile from shore on ridge at 75 ft. elevation (107 specimens, BPBM 166967, BPBM 166969, BPBM 166996).

**Remarks.**—The similarity of *Sinployea recurva* to the Austro-Zelandic flammulinid taxa with reduced ribbing is striking, but the probabilities are that this is convergent. *Sinployea angularis* is intermediate in sculpture between *S. recurva* and the Fijian charopids with typical sculpture, so that I have no hesitation in considering it to be a local development. No soft parts were available for dissection.

No other Charopidae covered in this monograph has such sculptural reduction. Although many species have the ribbing extremely irregular, such Fijian

shells as *S. irregularis* (fig. 65d-f) and *Ba humbugi* (fig. 74a-c) being good examples, the almost complete loss of ribbing does not occur. This condition is more common in the Endodontidae, where a number of *Endodonta*, several *Nesodiscus*, one *Nesophila*, and one *Libera* have undergone such reduction. In all of these cases, the shells are quite large, and sculptural reduction is associated with size increase. The name *recurva* refers to the reduced shell sculpture on the lower whorls in particular, indicating a return to simplified shell structure.

I suspect it may be an arboreal or semiarboreal species.

***Sinployea princei* (Liardet, 1876). Figure 65a-c.**

*Helix princei* Liardet, 1876, Proc. Zool. Soc. London, 1876, p. 100, pl. 5, fig. 4, a—Taveuni Island, Fiji Islands.

*Patula princei* (Liardet), Garrett, 1887, Proc. Zool. Soc. London, 1887, p. 179.

*Helix (Patula) princei* Liardet, Tryon, 1887, Man. Conchol., (2) 3, p. 27, pl. 5, fig. 83a.

*Endodonta (Charopa) princei* (Liardet), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Charopa princei* (Liardet), Gude, 1913, Proc. Malacol. Soc. London, 10, (5), p. 330; Germain, 1932, Ann. Inst. Ocean., 12 (2), p. 45.

**Diagnosis.**—Shell small, diameter 2.35–2.68 mm. (mean 2.43 mm.), with  $3\frac{1}{2}$ – $4\frac{1}{8}$  rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion more than  $\frac{1}{8}$  body whorl width, H/D ratio 0.524–0.586 (mean 0.551). Apical sculpture of 8–10 (mean 9.0) fine and relatively low spiral cords. Postnuclear sculpture of high, prominent, thin, protractively sinuated radial ribs, 80–102 (mean 91.1) on the body whorl, whose interstices are  $1\frac{1}{2}$ –3 times their width. Ribs/mm. 11.85–13.80 (mean 12.06). Microsculpture of fine radial riblets, 3–6 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets that are barely visible under 96 $\times$  magnification. Secondary spiral cording occasionally visible near periphery and shell base. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.74–4.83 times (mean 4.28) in the diameter, margins rounded. Whorls very strongly rounded, aperture circular, sometimes slightly flattened laterally above periphery, inclined about 20° from shell axis. Color reddish horn, no flammulations.

*Sinployea princei* is very similar to *S. inermis inermis* (fig. 66a-c), differing primarily in its much more crowded radial ribbing, greatly reduced secondary spiral cording, and slightly smaller size. *Sinployea lauensis* (fig. 68a-c) is larger, flatter, and has a distinctly less protruding spire. Other Fijian species differ greatly in rib spacing and count. *Sinployea ellicensis* (fig. 62a-f) has a flammulated color pattern, much more prominent secondary spiral cording, and averages three-eighths of a whorl less.

**Description.**—Shell small, with  $3\frac{3}{4}$  moderately tightly coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending more rapidly, H/D ratio 0.545. Apical whorls  $1\frac{1}{8}$ , sculpture of 8 narrow, widely spaced spiral ribs with faint traces of weaker radial riblets on last eighth whorl. Postnuclear whorls with narrow, lamellar, somewhat crowded, slightly protractively sinuated radial ribs, 102 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of weak radial and finer spiral riblets with a secondary sculpture of weak, widely spaced spiral cords visible only on periphery and base of body whorl. Sutures deep, whorls strongly rounded above, evenly rounded on outer and basal margin. Color light reddish yellow-horn without darker markings. Umbilicus narrow, U-shaped, regularly decoiling, contained 4.08 times in the

diameter. Aperture subcircular with evenly rounded outer margin, inclined about 15° from the shell axis. Height of lectotype 1.28 mm., diameter 2.36 mm.

**Lectotype.**—Fiji: Taveuni Island. Collected by Liardet. BMNH 76.9.9.2.

**Range.**—Taveuni and Kandavu, Fiji Islands.

**Paratypes.**—BMNH 76.9.9.2.

**Material.**—Fiji (2 specimens, Brussels): Taveuni (6 specimens, Zurich); Kandavu (4 specimens, FMNH 48997, SMF 165749).

**Remarks.**—Specimens from Kandavu, originating from the Rolle collection, are separable (table XXX) from the Taveuni specimens only by their narrower umbilicus. They are considered to be *S. princei*, but were not included in figuring mean size because I am uncertain that the locality is accurate.

No material of *S. princei* has been collected in this century.

***Sinployea inermis* (Mousson, 1870).**

Several populations from islands in the Lau Group are considered to be conspecific. They differ from the Taveuni and Kandavu *S. princei* (fig. 65a-c) in their higher spire protrusion and much less crowded radial ribbing (fig. 66a-e). Lau Archipelago species of similar size, *S. lauensis* (fig. 68a-c) and *S. navutuensis* (fig. 68d-f), plus the Viti Levu *S. godeffroyana* (fig. 69a-c), all have much more numerous and crowded radial ribbing plus moderately to greatly different proportions. Extralimital species such as the Tongan *S. vicaria* (fig. 58a-c) and Ellice Island *S. ellicensis* (fig. 62a-c) differ in details of sculptural character and spacing, but obviously are closely related.

Variation among populations on the same island and from different islands is relatively extensive (tables XXXII–XXXVI) and somewhat difficult to interpret. Available material was collected in the 1850s, 1860s, in 1934, 1938, 1973, and 1977. Since the Lau Group has unpredictable periods of drought, the possibility of ecophenotypic dwarfing must be considered in accessing the mean differences. Most samples fit relatively well into one of three geographic variation patterns that are considered to represent subspecies. Specimens from the northern group of Vanua Mbalavu, Mango, and Kimbombo Islands are nearest to *S. princei*, having more ribs and intermediate umbilical width (fig. 66a-c). They average about nine apical cords. Samples from the large, centrally located island of Lakemba vary in umbilical width but average a narrow umbilicus, 11.6 apical cords, and have very widely spaced and large radial ribs (fig. 66e). Those from the more southerly Lau Group, Aiwa, Yangasa Levu, and Navutu-i-Loma tend to have a slightly wider umbilicus, average 13.6 apical cords, have a little less crowded ribbing than those from the northern area, and are easily separable from the Lakemba populations (fig. 66d). Frequency distributions of the D/U ratio, ribs/mm., and ribs (tables XXXII–XXXIII) illustrate the extent of overlap for any single character. Rib



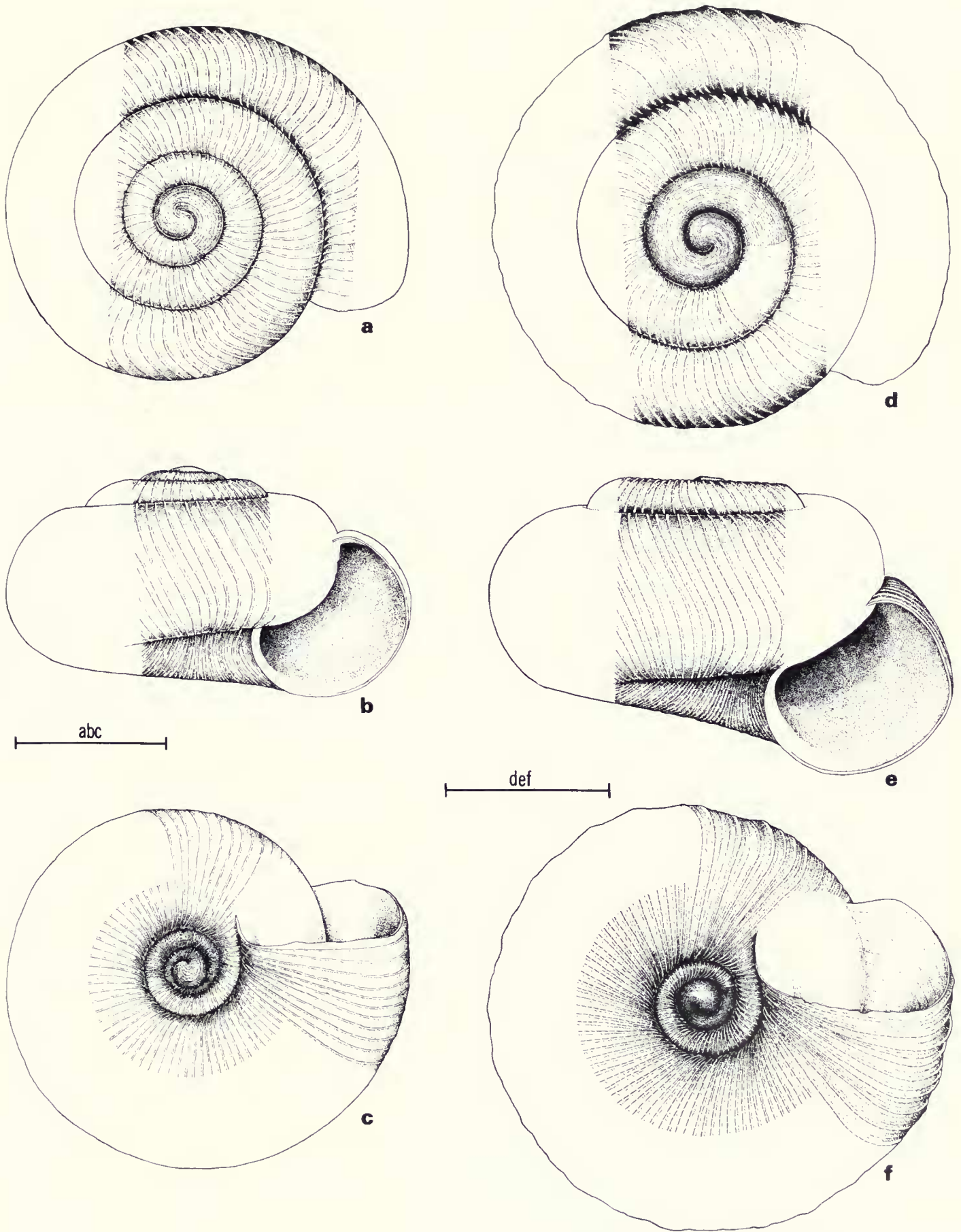


FIG. 65. a–c, *Sinployea princei* (Liardet). Taveuni, Fiji. Probable paratype. Zoologisches Institut der Universität Zurich, d–f, *Sinployea irregularis* (Garrett). Viti Levu, Fiji. Lectotype. BPBM 7982. Scale lines equal 1 mm. (MM).

TABLE XXXI. - LOCAL VARIATION IN FIJIAN, MELANESIAN AND MICRONESIAN SINPLYOEIA.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>angularis</u>						
Sta. 3 BPBM 166642	7	-----	-----	1.23±0.025 (1.10-1.28)	2.09±0.024 (2.01-2.17)	0.588±0.0121 (0.540-0.615)
Sta. 2 BPBM 166616	7	-----	-----	1.18±0.028 (1.07-1.28)	2.10±0.031 (2.02-2.25)	0.561±0.0090 (0.512-0.591)
<u>recurisa</u>						
Sta. 27 BPBM 166967	12	-----	-----	1.66±0.027 (1.52-1.85)	2.81±0.045 (2.62-3.11)	0.589±0.0066 (0.562-0.634)
<u>lauensis</u>						
Sta. 30 BPBM 167139	4	-----	-----	1.38±0.065 (1.19-1.49)	2.68±0.112 (2.42-2.95)	0.515±0.0110 (0.493-0.544)
Sta. 43 BPBM 167234	5	100.4±2.23 (95-105)	11.59±0.287 (10.96-12.62)	1.48±0.076 (1.39-1.79)	2.79±0.078 (2.65-3.08)	0.531±0.0143 (0.494-0.581)
Sta. 28, 29 BPBM 167020,-55	3	119	12.51	1.61±0.145 (1.32-1.79)	2.96±0.141 (2.68-3.15)	0.542±0.0242 (0.494-0.568)
<u>navutuensis</u>						
Sta. 29 ex BPBM 167020, ex BPBM 167055	4	142	11.64	1.32±0.73 (1.16-1.49)	2.66±0.048 (2.58-2.78)	0.498±0.0220 (0.449-0.556)
<u>kusaieana</u>						
Sta. 44 BPBM 155874-5,-7,-9	11	90.4±1.97 (84-103)	11.19±0.287 (9.96-13.17)	1.31±0.027 (1.18-1.48)	2.58±0.020 (2.50-2.73)	0.506±0.0074 (0.481-0.542)
<u>descendens</u>						
Karlei ZMB	24	91.7±1.55 (77-103)	13.07±0.232 (11.16-14.71)	1.16±0.009 (1.05-1.25)	2.25±0.013 (2.14-2.40)	0.515±0.0041 (0.470-0.548)
Matong ZMB	7	91.9±2.62 (80-99)	12.68±0.313 (11.33-13.73)	1.22±0.017 (1.15-1.27)	2.32±0.037 (2.15-2.43)	0.528±0.0062 (0.504-0.550)
<u>novopommerana</u>						
Karlei ZMB	12	93.8±3.29 (72-104)	12.71±0.499 (9.61-15.10)	1.21±0.044 (1.05-1.61)	2.33±0.059 (2.11-2.85)	0.520±0.0089 (0.467-0.567)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	
<u>angularis</u>						
Sta. 3		3 7/8+(3 3/4-4)	0.32±0.531 (0.23-0.36)	6.71±0.415 (5.81-8.71)	15	
Sta. 2		3 7/8-(3 3/4-4)	0.38±0.007 (0.35-0.39)	5.57±0.099 (5.21-6.05)	-----	
<u>recurisa</u>						
Sta. 27		3 7/8-(3 1/2-4 1/8)	0.42±0.015 (0.33-0.49)	6.70±0.211 (5.78-7.90)	16.5±1.50 (15-18)	
<u>lauensis</u>						
Sta. 30		3 5/8+(3 1/2-3 7/8)	0.61±0.039 (0.53-0.70)	4.40±0.120 (4.15-4.65)	-----	
Sta. 43		3 7/8(3 3/4-4 1/8)	0.68±0.030 (0.63-0.79)	4.10±0.085 (3.88-4.32)	-----	
Sta. 28		4 1/8(3 7/8-4 1/4)	0.69±0.038 (0.63-0.76)	4.26±0.150 (4.00-4.52)	-----	
<u>navutuensis</u>						
Sta. 29		4 1/8(4-4 3/8)	0.78±0.016 (0.76-0.82)	3.38±0.055 (3.25-3.52)	10.0±1.00 (9-11)	
<u>kusaieana</u>						
Sta. 44		4-(3 3/4-4 1/8)	0.74±0.009 (0.69-0.79)	3.51±0.038 (3.21-3.67)	9.2±0.20 (8-10)	
<u>descendens</u>						
Karlei		4 1/8+(4-4 1/4)	0.83±0.011 (0.76-0.95)	2.73±0.029 (2.43-2.94)	10.7±0.30 (9-14)	
Matong		4 3/8-(4 1/8-4 1/2)	0.85±0.028 (0.74-0.95)	2.73±0.046 (2.55-2.91)	10.5±0.29 (10-11)	
<u>novopomm.</u>						
Karlei		3 3/4(3 1/2-4 1/8)	0.67±0.028 (0.54-0.92)	3.49±0.076 (3.09-3.96)	10.7±0.36 (10-12)	



TABLE XXXII. - D/U RATIO FREQUENCY IN *SINPLOYEA INERMIS* SUBSPECIES.

D/U Ratio	<u><i>S.inermis</i></u> <u><i>inermis</i></u>	<u><i>S.inermis</i></u> <u><i>meridionalis</i></u>	<u><i>S.inermis</i></u> <u><i>lakembana</i></u>
3.00-3.39		7	
3.40-3.79	7	17	1
3.80-4.19	17	2	2
4.20-4.59	17		
4.60-4.99	6		2
5.00-5.39			
5.40-5.79			
5.80-6.19			3
6.20-6.59			3
6.60-6.99			2
7.00-7.39			1

differences are somewhat obscured by the strong tendency for gerontic crowding and irregularity of rib growth in most adult specimens. The differences are much clearer on the penultimate and first part of the body whorl, but convenient quantification of data from this section of the shell was not achieved. Most specimens are readily assignable to one of the three groups. Hence, recognition of three subspecies is proposed: *Sinployea inermis inermis* from Vanua Mbalavu, Kimbombo, and Mango; *S. i. lakembana* from Lakemba; and *S. i. meridionalis* from Aiwa, Navutu-i-Loma, and Yangasa Levu.

Larger collections from more islands may result in altering this classification. The apical cording counts and the size differences in ribbing are substantial. Pos-

TABLE XXXIV. - RIB FREQUENCY IN *SINPLOYEA INERMIS* SUBSPECIES.

Ribs	<u><i>S.inermis</i></u> <u><i>inermis</i></u>	<u><i>S.inermis</i></u> <u><i>meridionalis</i></u>	<u><i>S.inermis</i></u> <u><i>lakembana</i></u>
35-41			1
42-48			3
49-55		1	7
56-62		2	4
63-70	5	3	
71-77	6	3	
78-84	8	3	
85-91			
92-98	1		
99-105	3	1	

sibly specific level differentiation is involved, but the presence of samples not clearly referable to a subspecies and the amount of overlap (tables XXXII-XXXVI) suggest conservative treatment.

The specimens collected from "Vatou Island" (=Vanua Vatu) during the surveys of the *Herald* in the mid-1850s are still preserved in the British Museum (Natural History) (BMNH 59.1.14.63). Only one fully adult shell is in good condition, but in general appearance the specimens are intermediate between subspecies *inermis* and subspecies *lakembana*. They have the relatively widely spaced ribbing that is characteristic of *meridionalis* and *lakembana*, although somewhat more crowded than typical examples of either subspecies. The umbilicus varies widely in width from the narrow type of *lakembana* to the widely opened umbilicus of *meridionalis*.

Single shells from two islands lying within the range of *S. i. meridionalis* could not be assigned to a subspecies with assurance. Their measurements are given in Table XXXVI. The Ongea example (BPBM 161228) has a narrower umbilicus than does the nominate race or any specimens of *S. i. meridionalis* but disagrees in sculpture and apical cording with *S. i. lakembana*. An adult shell from Tavu-na-Sithi (BPBM 78805) could be referred to either typical *inermis* or *meridionalis*. It has the umbilical size of *inermis*, but the ribbing is closer to that of *meridionalis*. Collection of adequate samples is needed in order to establish the position of these populations.

Derivation of *S. adposita* (fig. 69d-f) from *S. inermis* requires size increase, greater protrusion of the spire and its correlated narrowing of the umbilicus, plus greater spacing of the ribs. Similarly, increase in body whorl descension and development of ribbing irregularity would be sufficient to derive *S. irregularis* (fig. 65d-f) from either *S. inermis* or *S. princei*.

The penis of *Sinployea inermis* is slightly more than half the size of the penis in *S. adposita* and differs radically in shape and internal proportions. The vergic

TABLE XXXIII. - RIBS/MM. FREQUENCY IN *SINPLOYEA INERMIS* SUBSPECIES.

Ribs/mm.	<u><i>S.inermis</i></u> <u><i>inermis</i></u>	<u><i>S.inermis</i></u> <u><i>meridionalis</i></u>	<u><i>S.inermis</i></u> <u><i>lakembana</i></u>
4.50-4.99			1
5.00-5.49			
5.50-5.99			1
6.00-6.49			1
6.50-6.99		1	3
7.00-7.49		2	4
7.50-7.99	1	3	4
8.00-8.49	1	3	1
8.50-8.99	5		
9.00-9.49	2	1	
9.50-9.99	5	2	
10.00-10.49	2		
10.50-10.99	4		
11.00-11.49	2		
11.50-11.99	1	1	

TABLE XXXV. - LOCAL VARIATION IN *SINPLOYEA INERMIS*, I.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u><i>inermis inermis</i></u>					
Vanua Mbalavu Sta. 70, 72 (1938)	6	75.3±5.37 (65-83)	1.28±0.020 (1.23-1.36)	2.28±0.013 (2.25-2.32)	0.562±0.0061 (0.544-0.586)
Sta. 69 (1938) BPBM 179396	10	76.3±1.33 (75-79)	1.36±0.032 (1.19-1.56)	2.39±0.029 (2.28-2.55)	0.570±0.0094 (0.514-0.627)
Ex Fulton BPBM 167433	5	78.0±8.61 (65-102)	1.48±0.058 (1.36-1.66)	2.52±0.067 (2.38-2.78)	0.585±0.0134 (0.547-0.627)
Mango Sta. 89 (1938) BPBM 179941	6	78.0±2.01 (76-80)	1.40±0.065 (1.19-1.62)	2.56±0.064 (2.32-2.78)	0.546±0.0127 (0.506-0.583)
Sta. 91 (1938) BPBM 180025-6	14	91.5±4.72 (77-104)	1.67±0.032 (1.46-1.85)	2.95±0.033 (2.75-3.08)	0.564±0.0075 (0.530-0.629)
Kimbombo Bryan! (1924) BPBM 79103	4	79	1.45±0.067 (1.32-1.59)	2.64±0.140 (2.28-2.88)	0.565±0.0065 (0.558-0.580)
<u><i>inermis meridionalis</i></u>					
Yangasa Levu Sta. 30 (1934) BPBM 167138	10	72	1.81±0.037 (1.59-1.95)	3.04±0.029 (2.95-3.25)	0.595±0.0149 (0.505-0.655)
Aiwa Sta. 40 (1934) BPBM 167209	4	93.0±11.03 (82-104)	1.66±0.027 (1.59-1.72)	2.96±0.109 (2.72-3.21)	0.562±0.0205 (0.521-0.610)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u><i>i. inermis</i></u>					
Mbalavu Sta. 70, 72	3 5/8+(3 1/2-3 7/8)		0.53±0.013 (0.49-0.59)	4.27±0.094 (3.89-4.60)	8.00±0.71 (7-10)
Sta. 69	3 7/8(3 5/8-4 1/4)		0.58±0.016 (0.49-0.66)	4.09±0.098 (3.50-4.60)	9.38±0.26 (8-10)
Ex Fulton	4-(3 7/8-4 1/8)		0.57±0.026 (0.53-0.66)	4.45±0.112 (4.17-4.69)	8.33±1.20 (6-10)
Mango Sta. 89	4 1/8+(3 7/8-4 1/2)		0.65±0.034 (0.53-0.72)	3.94±0.139 (3.55-4.38)	9
Sta. 91	4 1/4-(4-4 5/8)		0.70±0.017 (0.63-0.82)	4.20±0.081 (3.68-4.65)	9.57±0.37 (8-11)
Kimbombo Bryan!	3 7/8-(3 1/2-4 1/8)		0.63±0.087 (0.49-0.79)	4.15±0.260 (3.58-4.60)	9
<u><i>i. merid.</i></u>					
Yangasa Sta. 30	4 3/8+(4 1/4-4 5/8)		0.87±0.025 (0.72-0.99)	3.50±0.092 (3.27-4.14)	12.00±0.58 (11-13)
Aiwa Sta. 40	4 1/4-(4-4 1/4)		0.81±0.044 (0.69-0.89)	3.57±0.013 (3.54-3.60)	-----

papilla in the former is about a third of the size of the latter, and the muscular collar is larger both actually and proportionately. *Sinployea adposita* has the stimulatory pad smaller and shorter than in *S. inermis*. The latter has a much broader penis that is wider medially than apically and then tapers abruptly to atrium. *Sinployea adposita* has the penis enlarged apically and medially, then it tapers gradually to atrium.

***Sinployea inermis inermis* (Mousson, 1870). Figures 66a-c, 67e.**

*Patula (Patula) inermis* Mousson, 1870, J. de. Conchyl., 18, pp. 118-119, pl. 7, fig. 7—Lomma-Lomma on Vanua-Balavo, Lau Group, Fiji Islands.

*Helix inermis* (Mousson), Pfeiffer, 1876, Monog. helic. viv., 7, p. 167.

*Patula inermis* Mousson, Garrett, 1887, Proc. Zool. Soc. London, 1887, p. 178.



TABLE XXXVI. - LOCAL VARIATION IN *SINPLOYEA INERMIS*, II.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u><i>inermis meridionalis</i></u>					
Navutu-I-Loma Sta. 28-9(1934) BPBM 167019, -55-6	12	68.0±3.16 (53-83)	1.48±0.39 (1.32-1.69)	2.72±0.047 (2.52-3.05)	0.544±0.0087 (0.500-0.595)
<u><i>inermis lakembana</i></u>					
Lakemba Sta. 42(1934) BPBM 167222	4	54.8±4.61 (42-62)	1.48±0.083 (1.32-1.66)	2.58±0.111 (2.38-2.88)	0.574±0.0195 (0.552-0.633)
Sta. 97(1938) BPBM 180101	10	49.5±1.71 (38-59)	1.36±0.025 (1.19-1.49)	2.29±0.028 (2.15-2.38)	0.594±0.0085 (0.545-0.634)
Transitional Sets					
Vatou BMNH 59.1.14. 63	5	65.8±3.40 (59-70)	1.33±0.093 (1.13-1.61)	2.42±0.100 (2.19-2.73)	0.548±0.0177 (0.518-0.616)
Ongea	1	83	1.41	2.66	0.531
Tavua-na- Sithi	1	75	1.58	2.70	0.586
		WHORLS	UMBILICUS	D/U RATIO	APICAL RIBS
<u><i>i. iner.</i></u>					
Navutu Sta. 28-29	4	1 1/8+(3 7/8-4 1/2)	0.78±0.021 (0.69-0.92)	3.50±0.055 (3.07-3.81)	11.43±0.68 (9-14)
<u><i>i. lakem.</i></u>					
Lakemba Sta. 42	4	1 1/8+(3 7/8-4 1/2)	0.62±0.049 (0.53-0.76)	4.21±0.251 (3.78-4.93)	-----
Sta. 97	4	-(3 3/4-4 1/8)	0.37±0.015 (0.33-0.49)	6.24±0.206 (4.73-7.10)	13.57±0.72 (11-16)
Transitional					
Vatou	4	(3 7/8-4 1/4)	0.57±0.026 (0.49-0.66)	4.30±0.375 (3.32-5.53)	-----
Ongea	3	3/4	0.56	4.77	8
Tavua.	4	1/4 -	0.66	4.10	-----

*Helix (Patula) inermis* (Mousson), Tryon, 1887, Man. Conchol., (2) 3, p. 41, pl. 8, figs. 60-61.

*Endodonta (Charopa) inermis* (Mousson), Pilsbry, 1893, Man. Conchol. (2) 9, p. 35.

*Charopa inermis* (Mousson), Gude, 1913, Proc. Malacol. Soc. London, 10 (5), p. 330—Vatou (Herald Expedition!); Germain, 1932, Ann. Inst. Ocean., 12 (2), p. 45.

*Diagnosis*.—Shell relatively small, diameter 2.24–3.06 mm. (mean 2.60 mm.), with 3½–4% normally coiled whorls. Apex and spire usually moderately and evenly elevated, last whorl descending moderately to much more rapidly, spire protrusion about ½ body whorl width, H/D ratio 0.500–0.629 (mean 0.562). Apical whorls with 6–11 (mean 8.96) prominent spiral cords. Postnuclear whorls with high, prominent, narrow, strongly protractively sinuated radial ribs, 65–104 (mean 80.0) on the body whorl, whose interstices are 3–6 times their width. Ribs/mm. 8.39–11.75 (mean 9.82). Microsculpture

of very fine radial riblets, 6–12 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets and a few widely spaced secondary spiral cords. Umbilicus open, U-shaped, last whorl decoiling much more rapidly, contained 3.47–4.69 times (mean 4.17) in the diameter, margins rounded. Sutures and whorl contours typical, color reddish yellow-horn without separate flammulations.

*Sinployea inermis inermis* (fig. 66c) has a narrower umbilicus and more crowded major radial ribbing than *S. i. meridionalis* (fig. 66d); *S. i. lakembana* (fig. 66e) has much coarser and more widely spaced major radial ribs. Other Fijian species of similar size, *S. princei*, *S. lauensis*, and *S. navutuensis*, differ in proportions (table XXX) and/or ribbing. The Tongan *S. vicaria* (fig. 58a–c) has a higher spire and much more crowded sec-

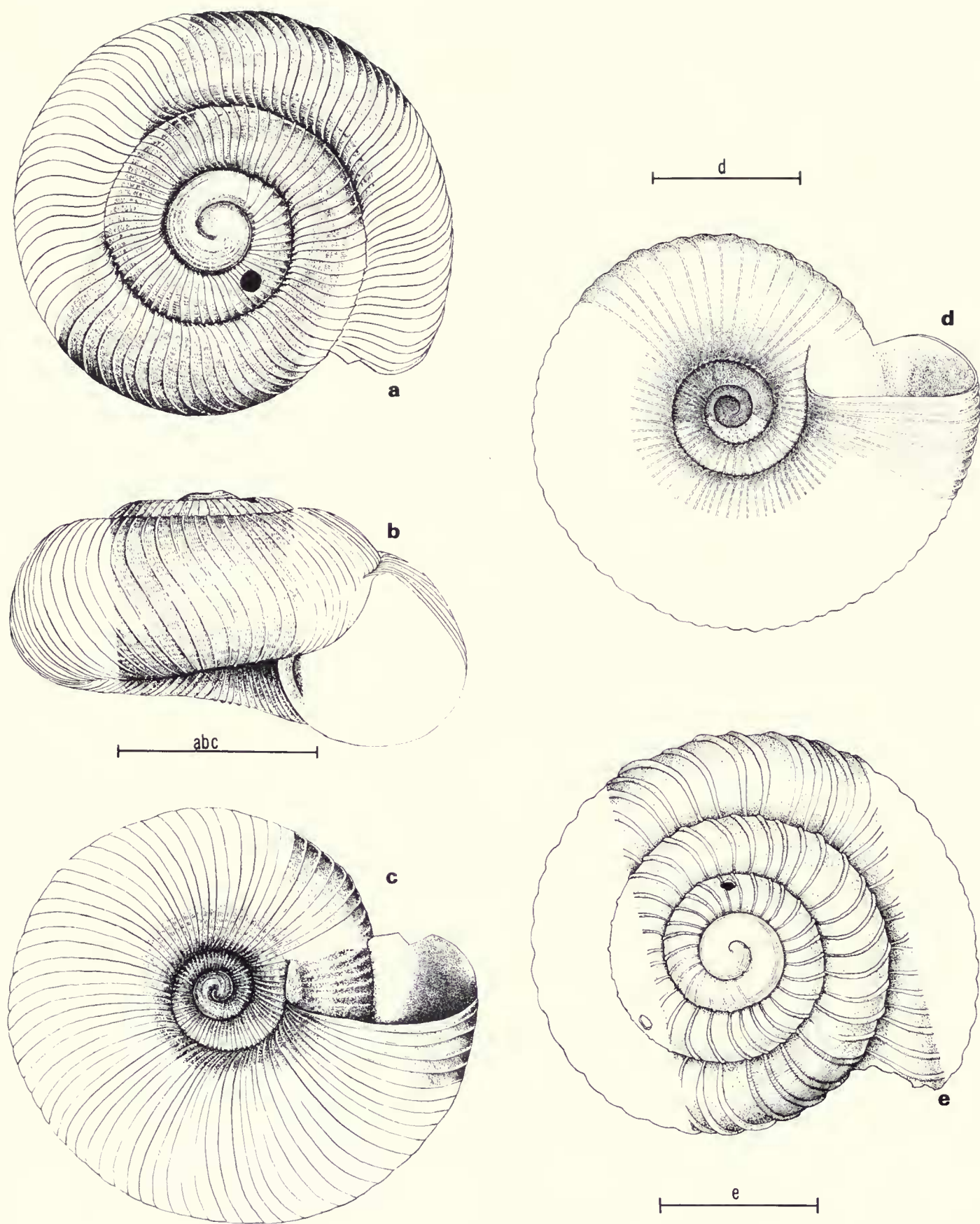


FIG. 66. a–c, *Sinployea inermis inermis* (Mousson). Station 72, Lomaloma, Vanua Mbalavu, Lau, Fiji. BPBM 179460; d, *Sinployea inermis meridionalis*, new subspecies. Station 30, Yangasa Levu, Lau, Fiji. Holotype. BPBM 167138; e, *Sinployea inermis lakembana*, new subspecies. Station 42, Lakemba, Lau, Fiji. Holotype. BPBM 167222. Scale lines equal 1 mm. (a–c, SH. d–e, MM).



ondary spiral cording in addition to the much more crowded radial ribbing.

*Description.*—Shell relatively small, with slightly less than 4½ normally coiled whorls. Apex barely emergent, upper spire flat, body whorl descending moderately sharply, H/D ratio 0.515. Apical whorls 1½, sculpture partially eroded with traces of 7 fine, rather widely spaced spiral ribs remaining. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, 69 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of very fine radial riblets, 4–6 between each pair of major ribs, crossed by even finer, more crowded spiral riblets with a secondary sculpture of moderately prominent, widely spaced spiral cords developed. Sutures deep, whorls strongly rounded above, moderately flattened laterally above periphery and on basal margin. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.47 times in the diameter, rounded margins. Color light reddish brown. Aperture ovate, lip slightly deflected above, flattened laterally above periphery and on basal margin, inclined about 20° from the shell axis. Height of lectotype 1.38 mm., diameter 2.58 mm.

*Lectotype.*—Fiji: Lau Group, Vanua Mbalavu. Collected by Dr. Graeffe. JDCP 3214.

*Range.*—Vanua Mbalavu, Mango, Kimbombo, Tuvutha, Lau Group, Fiji.

*Paratypes.*—Zurich, FMNH 116998.

*Material.*—Vanua Mbalavu (6 specimens, BPBM 167433): Lomaloma (9 specimens, Zurich, J. de Conchyl., FMNH 116998); north end Lomaloma (Station 69) 10–12 ft. inland at 3 ft. elevation (28 specimens, BPBM 179396, BPBM 179398, BPBM 179399); back of Lomaloma (Station 67) ½–¾ mile inland, 250–700 ft. elevation (8 specimens, BPBM 179379); south end Lomaloma (Station 72) 15 ft. inland at 3 ft. elevation (14 specimens, BPBM 179460, BPBM 179461); south end Unione Village (Station 70) 10 ft. inland at 3 ft. elevation (2 specimens, BPBM 179426); between Valika and Mosomo Bay (Station 78) ¾ mile inland at 200–250 ft. elevation (3 specimens, BPBM 179584, BPBM 179585); Station F-8, 300 ft. elevation, 1½ miles inland, northwest area (6 specimens, FMNH 168161). Mango Island: Marona (Station 92) 100 yd. inland at 10 ft. elevation (2 specimens, BPBM 180047); south-southwest from Marona (Stations 89, 90) about ½–¾ mile inland at 200–400 ft. elevation (15 specimens, BPBM 179941, BPBM 179975, BPBM 179988); ¾–1 mile southwest of Marona (Station 91) 1–50 yd. inland, at 5–30 ft. elevation (82 specimens, BPBM 180025–9). Kimbombo: East Islet, 100 yd. inland at 50–150 ft. elevation (28 specimens, BPBM 79079, BPBM 79103). Tuvutha: west coast (Station F-7) at 100 ft. elevation (5 specimens, FMNH 193768).

*Remarks.*—The specimens of *Sinployea inermis* from Vanua Mbalavu, Mango, and Kimbombo agree in sculpture and umbilical proportion, although exhibiting slight differences in size (table XXXV). Shells from Vanua Mbalavu are small, whereas those from Kimbombo and Mango are slightly to distinctly larger. On Mango, two populations were sampled. Shells from Station 89 (½–¾ mile south-southwest of Marona at 350–400 ft. elevation) were dead. They are noticeably smaller and with fewer radial ribs than

those from Station 91 (¾–1 mile southwest of Marona at 5–30 ft. elevation), which were collected alive. The latter sample contained a higher proportion of gerontic individuals, whereas the Station 89 material was barely adult. The Mango specimens are larger than those from Vanua Mbalavu, but no hesitation is felt in referring them to the same subspecies.

Material from both Mango (BPBM 180025) and Vanua Mbalavu (BPBM 179396) was dissected. Only differences are noted below.

*Description of soft parts.*—Pallial region typical, arms of kidney subequal, rectal slightly longer, maximum length 1.7 mm., slight strip of lung roof visible between ureter arms.

Genitalia (fig. 67e) typical, free oviduct slightly more slender than usual. Penis (P) about 0.8–1.0 mm. long, greatly swollen medially. Internally with very tiny vergic papilla surrounded by a heavy muscular collar. Stimulatory pad very large, walls below pad with obscure pilasters.

### *Sinployea inermis meridionalis*, new subspecies. Figure 66d.

*Diagnosis.*—Shell of average size, diameter 2.50–3.22 mm. (mean 2.88 mm.), with 3½–4½ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending moderately to much more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.505–0.655 (mean 0.566). Apical sculpture of 9–14 (mean 11.6) prominent, but narrow spiral cords. Postnuclear sculpture of narrow, prominent, protractively sinuated, rather widely spaced radial ribs, 53–104 (mean 72.2) on the body whorl, whose interstices are 3–7 times their width. Ribs/mm. 6.75–11.70 (mean 8.37). Microsculpture of very fine radial riblets, 8–12 between each pair of major ribs, crossed by barely visible spiral riblets, with a weak secondary sculpture of fine and widely spaced spiral cords that varies in frequency and prominence. Umbilicus broadly U-shaped, last whorl decoiling much more rapidly, contained 3.07–3.81 times (mean 3.51) in the diameter, margins rounded. Whorls strongly flattened laterally above periphery, aperture subcircular, inclined about 20° from shell axis.

*Sinployea inermis meridionalis* (fig. 66d) has a wider umbilicus and more widely spaced major radial ribbing than the nominate race; *S. i. lakembana* (fig. 66e) is smaller, has a narrower umbilicus, and much more widely spaced radial ribbing. *Sinployea vicaria paucicosta* (fig. 58d) from Tonga is smaller, has the spire protruding further, and has a narrower umbilicus.

*Description.*—Shell slightly smaller than average, with 4½ relatively tightly coiled whorls. Apex barely elevated, lower whorls descending slowly, body whorl more rapidly, H/D ratio 0.565. Embryonic whorls 1½, sculpture of 11 relatively fine spiral ribs with an intrusion of faint radial ribbing on the last quarter whorl. Remaining whorls with rounded, prominent, protractively sinuated radial ribs, 67 on the body whorl, whose interstices are about 3–6 times their width. Microsculpture of very fine radial riblets, 8–12 between each pair of major ribs, with exceedingly fine, inconspicuous spiral riblets and a secondary sculpture of low, broadly rounded, relatively widely spaced spiral cords. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above peripheral margin, slightly compressed basally. Umbilicus broadly open, last whorl decoiling more rapidly, contained 3.29 times in the diameter. Color light yellow-reddish brown without darker flammulations. Aperture circular, strongly flattened laterally above periphery, with sharply rounded umbilical basal margin, inclined about 10° from the shell axis. Height of holotype 1.71 mm., diameter 3.03 mm.

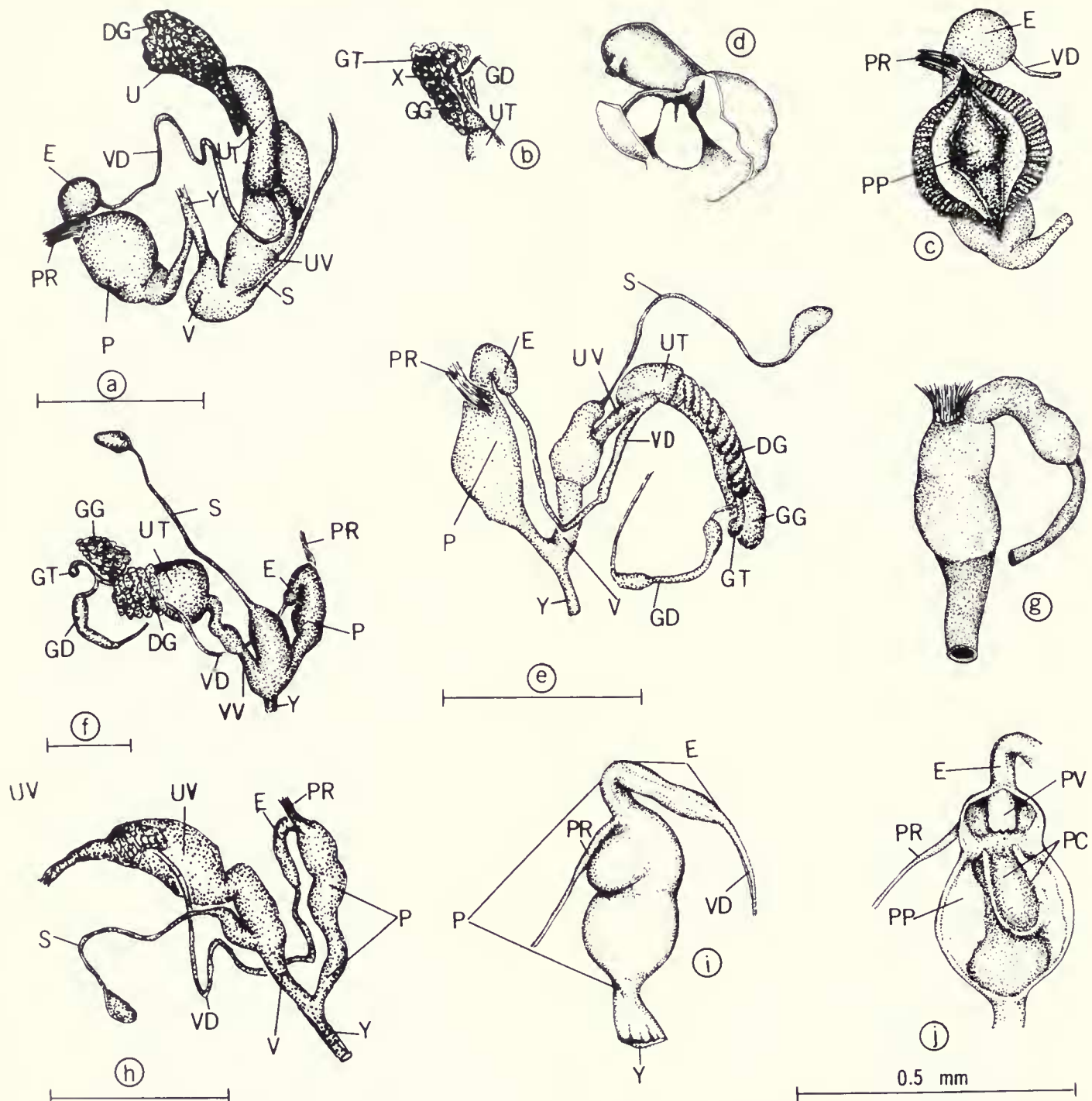


FIG. 67. Anatomy of Fijian, Caroline Island, and New Hebridean *Sinployea*: a-d, *Sinployea irregularis* (Garrett). Station 118, Nandarivatu, Viti Levu, Fiji. BPBM 178897. a, genitalia. b, detail of talon-carrefour region. c, partial view of penis interior. d, apical part of penis interior; e, genitalia of *Sinployea inermis inermis* (Mousson). Station 91, Marona, Mango Island, Lau, Fiji. BPBM 180025; f, genitalia of *Sinployea inermis lakembana*, new subspecies. Station 97, Toumba, Lakemba Island, Lau, Fiji. BPBM 180101; g, penis and epiphallus of *Sinployea adposita* (Mousson). Station 97, Toumba, Lakemba Island, Lau, Fiji. BPBM 180099; h, genitalia of *Sinployea kusaieana*, new species. Station 44, Lele Islet, Kusaie, Caroline Islands. BPBM 155874; i-j, *Sinployea euryomphala* (Solem). Espiritu Santo, New Hebrides. FMNH 109493. (a-c, e-f, h, MO; d, MM; g, JC; i-j, PS).

**Holotype.**—Fiji: Lau Group, Yangasa Levu, Station 30, hillside on south end of island, 150 ft. inland at 40 ft. elevation. Collected by H. S. Ladd on July 26, 1934. BPBM 167138.

**Range.**—Yangasa Levu, Navutu-i-Loma, and Aiwa, Lau Group, Fiji.

**Paratypes.**—Yangasa Levu: hillside at south end of island (Station 30), 150 ft. inland at 40 ft. elevation (96 specimens, BPBM 167138). Aiwa: Vataniyambia on southwest quarter (Station 40) of island, about 50 yd. inland at 25 ft. elevation (20 specimens, BPBM 167209). Navutu-i-Loma: ridge on northeast quarter of



island (Stations 28, 29), about 150 yd. inland at 100 ft. elevation (52 specimens, BPBM 167019, BPBM 167056, BPBM ex 167055).

**Remarks.**—The shells of *Sinployea inermis meridionalis* from Navutu-i-Loma are distinctly smaller and more depressed in H/D ratio than are those from Aiwa or Yangasa Levu (tables XXXV–XXXVI). Shells from Aiwa have a much higher rib count. Comparatively few of the examples were adult or whole enough to measure, so that the significance of this data is uncertain. From Navutu-i-Loma there were 23.1% adults; from Aiwa 20%; and from Yangasa Levu only 10.3%. I would expect that the size difference is real, but more complete collections are required.

***Sinployea inermis lakembana*, new subspecies.** Figures 66e, 67f.

**Diagnosis.**—Shell small, diameter 2.14–2.86 mm. (mean 2.36 mm.), with  $3\frac{3}{4}$ – $4\frac{1}{2}$  rather tightly coiled whorls. Apex and spire moderately to strongly and evenly elevated, last whorl descending much more rapidly, spire protrusion more than  $\frac{1}{5}$  body whorl width, H/D ratio 0.508–0.634 (mean 0.583). Apical sculpture of 11–16 (mean 13.6) prominent spiral cords. Postnuclear sculpture of high, very prominent, sharply defined, protractively sinuated radial ribs, 38–64 (mean 51.3) on the body whorl, whose interstices are 4–6 times their width on the spire and first part of body whorl, becoming crowded and irregular on gerontic growth sections. Ribs/mm. 4.67–8.20 (mean 7.01). Microsculpture of extremely fine radial riblets, more than 10 between each pair of major ribs, but usually too fine for accurate counting at 96 $\times$  magnification, barely visible microspirals, and more prominent, rather widely spaced secondary spiral cording. Umbilicus variable in size, usually narrow, U-shaped, last whorl decoiling slightly to much more rapidly, contained 3.07–7.10 times (mean 5.54) in the diameter, margins strongly rounded. Sutures very deep, whorls shouldered above, compressed laterally above periphery and on basal margin, aperture inclined about 30° from shell axis.

*Sinployea inermis lakembana* has much stronger and more widely spaced major radial ribbing, plus a usually more strongly deflected body whorl and narrower umbilicus than either of the other races of *S. inermis* (fig. 66a–d). No other Fijian species has such strong ribbing that is so widely spaced.

**Description.**—Shell relatively small, with  $4\frac{1}{2}$  tightly coiled whorls. Apex very slightly elevated, lower spire and body whorl descending more rapidly, H/D ratio 0.552. Apical whorls  $1\frac{1}{2}$ , sculpture of 12 prominent spiral cords, surface partially eroded. Postnuclear whorls with prominent, relatively narrow, quite widely spaced radial ribs, 42 on the body whorl, whose interstices are 3–6 times their width. Microsculpture of extremely fine radial and even finer, more crowded spiral riblets, crossed by low, rounded, relatively closely spaced spiral cords. Sutures deeply impressed, whorls strongly rounded, only slightly flattened laterally above periphery and on basal margin. Color partially leached from shell. Umbilicus moderately widely open, U-shaped, last whorl decoiling more rapidly, contained 3.78 times in the diameter. Aperture circular, slightly flattened laterally above periphery, lip broken. Height of holotype 1.58 mm., diameter 2.86 mm.

**Holotype.**—Fiji: Lau Group, Lakemba, Station 42, Tambusue, west side near coast at 10 ft. elevation. Collected by H. S. Ladd on August 8, 1934. BPBM 167222.

**Range.**—Lakemba, Lau Group, Fiji.

**Paratypes.**—Lakemba (2 specimens, AIM, collected June 30, 1977, by W. Cernohorsky): Tambusue, west side near coast (Station 42) at 10 ft. elevation (3

specimens, BPBM 167222); west end of Toumba (=Tubou) (Station 97) to  $\frac{2}{5}$  mile away at 15 ft. elevation (10 specimens, BPBM 180101).

**Remarks.**—The holotype of *Sinployea inermis lakembana* is the largest and most widely umbilicated specimen seen, but was chosen because of the clear sculpture. Three sets were available, collected in different years from different portions of Lakemba. Shells taken on the west coast by Harry Ladd in 1934 (Station 42, BPBM 167222) are larger, less elevated, and more widely umbilicated (table XXXVI) than those found near Toumba (=Tubou) by Zimmerman and Kondo in 1938 (Station 97, BPBM 180101). Cernohorsky's 1977 specimens (Solem, 1978a) agree with the former examples. Apparently Ladd's Station 42 is the same as his geological Station L492, shown in Ladd & Hoffmeister (1945, p. 99, fig. 19). It was cited as "about 3 miles northwest of Tumbou" (Ladd & Hoffmeister, 1945, p. 190) and thus is separated by 2.6 miles from the later collection by Kondo and Zimmerman. Both sets contain only adults showing marked gerontic growth, so that the differences are not caused by age-biased samples. Further collections are needed to determine whether the differences are ecophenotypic or geographic in nature. With the umbilical variation showed by the Vanua Vatu material (table XXXVI), I suspect that there will be no systematic significance to this difference between the sets.

**Description of soft parts.**—Pallial region and external body features as in nominate subspecies. Genitalia (fig. 67f) without substantive differences, more swollen spermathecal base caused by presence of sperm packet. Shorter appearance of atrium (Y) caused by drawing a retracted specimen with atrium and vagina folded under edge.

(Based on BPBM 180101, 2 whole and several fragmentary examples.)

***Sinployea lauensis*, new species.** Figure 68a–c.

**Diagnosis.**—Shell slightly smaller than average, diameter 2.40–3.13 mm. (mean 2.76 mm.), with  $3\frac{1}{2}$ – $4\frac{1}{4}$  rather loosely coiled whorls. Apex and spire barely to moderately and evenly elevated, last whorl descending a little more rapidly, spire protrusion about  $\frac{1}{5}$  body whorl width, H/D ratio 0.493–0.581 (mean 0.530). Apical whorls with 9–11 (mean 9.6) fine spiral cords. Postnuclear sculpture of low, rounded, crowded, strongly protractively sinuated radial ribs, 95–119 (mean 103.9) on the body whorl, whose interstices are 1–2 times their width. Ribs/mm. 10.93–14.46 (mean 11.53). Microsculpture of fine radial riblets, 2–5 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, with fine, relatively crowded secondary spiral cording visible on spire and part of the body whorl. Umbilicus narrow, V-shaped, last whorl decoiling much more rapidly, contained 3.88–4.65 times (mean 4.24) in the diameter, margins rounded. Whorls strongly rounded above, moderately to strongly compressed laterally above periphery, aperture subcircular, inclined about 25° from shell axis. Color reddish horn, no darker markings.

*Sinployea lauensis* differs from *S. inermis* (fig. 66a–e) in its much less protruded spire, greater rib frequency, and V-shaped, much more rapidly decoiling umbilicus. *Sinployea princei* (fig. 65a–c) is smaller, has fewer ribs, and the whorls are more evenly rounded and tightly coiled, with the umbilicus decoiling more regularly.

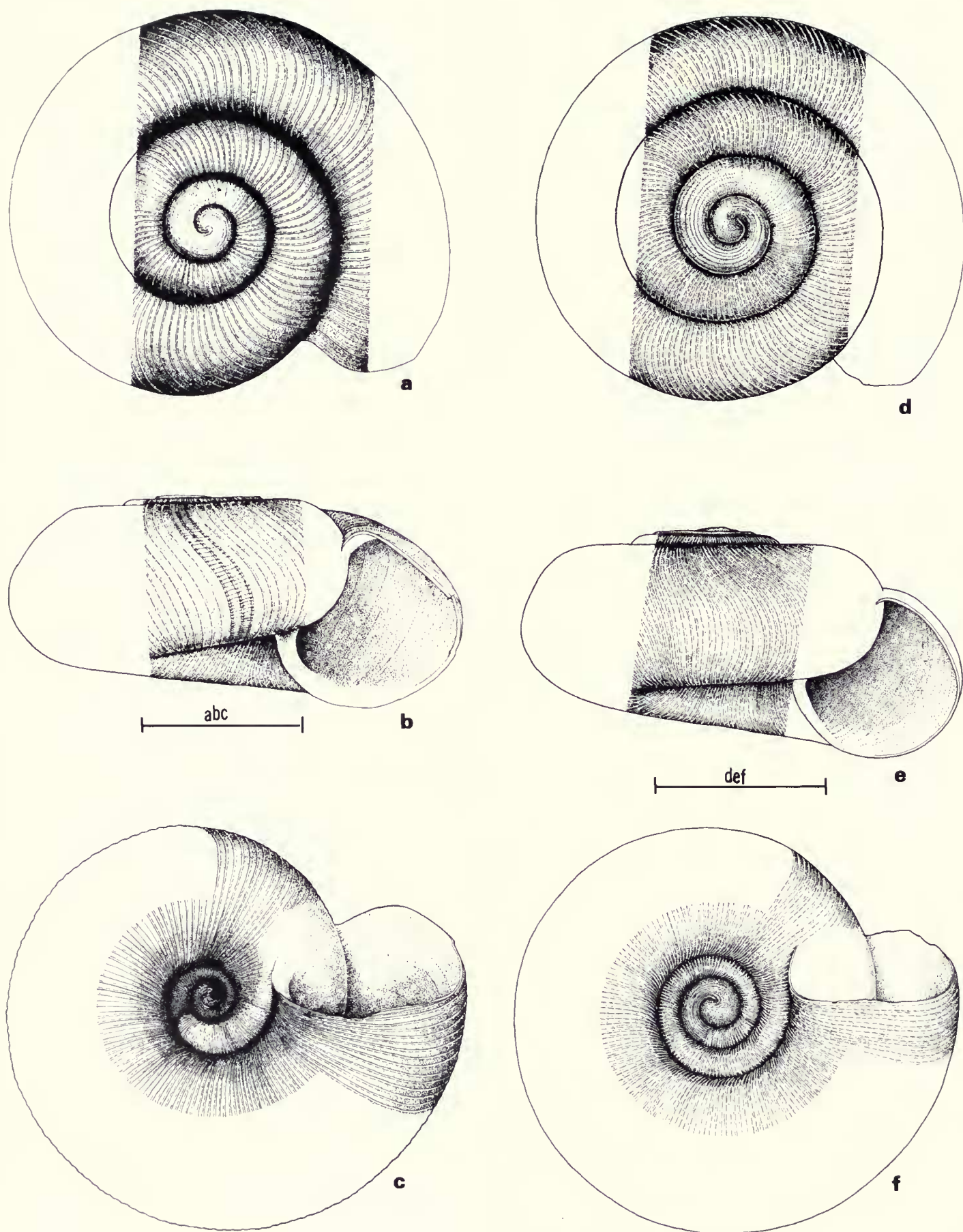


FIG. 68. a-c, *Sinployea lauensis*, new species. Station 43, Nayau, Lau, Fiji. Holotype. BPBM 167234; d-f, *Sinployea navutuensis*, new species. Station 29, Navutu-i-Loma, Lau, Fiji. Holotype. BPBM 9730. Scale lines equal 1 mm. (MM).



*Description*.—Shell of average size, with slightly less than 3¼ loosely coiled whorls. Apex and spire barely protruding, body whorl descending moderately, H/D ratio 0.494. Embryonic whorls 1½, sculpture of 9 very faint and widely spaced spiral cords. Remaining whorls with closely spaced, narrow, rounded, strongly protractively sinuated radial ribs, 103 on the body whorl, whose interstices are 1–2 times their width. Microsculpture of 3–6 fine radial riblets between each pair of major ribs, crossed by lower, more crowded spiral riblets, with some widely spaced narrow larger spiral cords. Sutures deeply impressed, whorls shouldered above, broadly flattened between shoulder and periphery, with slightly flattened basal margin. Umbilicus narrow internally, last whorl decoiling very rapidly, contained 4.05 times in the diameter. Color light reddish brown. Aperture subcircular, broadly flattened laterally above, inclined about 25° from the shell axis, with internal basal and columellar callus. Columellar margin of aperture slightly reflected. Height of holotype 1.38 mm., diameter 2.80 mm.

*Holotype*.—Fiji: Lau Group, Nayau Island, Station 43, ½ mile inland from Nauko at 250 ft. elevation. Collected at base of a limestone cliff by H. S. Ladd on August 13, 1934. BPBM 167234.

*Range*.—Nayau, Yangasa Levu, Namuka, Navutu-i-Loma, and Wangava, Lau Group, Fiji.

*Paratypes*.—Nayau: at base of limestone cliff (Station 43) ½ mile inland from Nauko at 250 ft. elevation (19 specimens, BPBM 167234). Namuka: southeast coast (Station F-3) at 50–75 ft. elevation (5 specimens, FMNH 168089). Yangasa Levu: hillside at south end of island (Station 30) 150 ft. inland at 40 ft. elevation (23 specimens, BPBM 167139). Navutu-i-Loma: ridge on northeast quarter of island (Stations 28, 30) 150 yd. inland at 150 ft. elevation (32 specimens, BPBM 167020, BPBM 167055). Wangava: northeast end of island (Stations 26, 27) 100 yd. inland at 10–15 ft. elevation (7 specimens, BPBM 166955, BPBM 166968, BPBM 166997); north end at 100 ft. elevation (38 specimens, FMNH 168092, FMNH 168101).

*Remarks*.—Individual specimens of *Sinployea lauensis* approach the measurements of *S. inermis meridionalis* for single characters (table XXX), but the different umbilical and whorl shape separate problem specimens. Typical examples are immediately separable on a number of characters. There is considerable similarity to the Samoan *Sinployea allecta* (fig. 54a–e) in general appearance, but that species is much more narrowly umbilicated and has less crowded radial ribbing.

Very little material was adult, and mean differences between the small samples from different islands are not statistically significant (table XXXI).

### *Sinployea navutuensis*, new species. Figure 68d–f.

*Diagnosis*.—Shell smaller than average, diameter 2.58–2.78 mm. (mean 2.66 mm.), with 4–4¾ normally coiled whorls. Apex and early spire flat to barely protruding, lower spire descending slightly, body whorl much more rapidly, spire protrusion ⅓ body whorl width, H/D ratio 0.449–0.556 (mean 0.498). Apical sculpture of 9–11 (mean 10.3) narrow but prominent spiral cords. Postnuclear whorls with narrow, crowded, fine, sharply outlined, protractively sinuated radial ribs, 121–147 (mean 136.7) on the body whorl, whose interstices are 1–2 times their width. Ribs/mm. 16.94–17.62 (mean 17.3). Microsculpture a lattice of barely visible radial riblets, 3–6 between each pair of major ribs, crossed by finer spiral riblets. A widely

spaced, fine sculpture of secondary spiral cording visible under angled lighting only. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 3.25–3.52 times (mean 3.38) in the diameter, margins rounded. Whorls strongly rounded, slightly compressed laterally above periphery and on basal margin, aperture circular, compressed laterally, inclined about 20° from shell axis.

The nearly flat apex, slight spire protrusion, wide umbilicus, and very crowded radial ribbing separate *Sinployea navutuensis* from the other Fijian species. *Sinployea lauensis* (fig. 68a–c) has a much narrower umbilicus, fewer and less crowded radial ribs, more loosely coiled whorls, and a wider body whorl. *Sinployea godeffroyana* (fig. 69a–c) is much smaller, much more elevated, has a narrower umbilicus, and even more crowded radial ribs. *Sinployea kusaieana* (fig. 63a–c) from the Caroline Islands is very similar in size and shape, but differs in having only 84–103 ribs on the body whorl and a slightly looser coiling pattern.

*Description*.—Shell smaller than average, with 4¾ moderately tightly coiled whorls. Apex and early spire barely elevated, body whorl descending moderately, H/D ratio 0.487. Embryonic whorls 1½, sculpture of 9 narrow, prominent spiral ribs. Postnuclear whorls with low, rounded, narrow, quite crowded, protractively sinuated radial ribs, 142 on the body whorl, whose interstices are about 1–2 times their width. Microsculpture of 3–5 very fine riblets between each pair of major ribs, crossed by much finer, lower, spiral riblets. Secondary sculpture of widely spaced, rounded spiral cords visible under good lighting. Sutures deep, whorls strongly rounded above, compressed laterally above periphery and slightly on basal margin. Umbilicus broadly cup-shaped, regularly decoiling, contained 3.39 times in the diameter. Color leached from shell. Aperture ovate, compressed laterally above periphery with gently rounded margin, inclined about 15° from the shell axis. Height of holotype 1.25 mm., diameter 2.57 mm.

*Holotype*.—Fiji: Lau Group, Navutu-i-Loma, Station 29, on ridge 150 yd. inland at 100 ft. elevation. Collected dead among limestone outcrops by H. S. Ladd on July 24, 1934. BPBM 9730.

*Range*.—Navutu-i-Loma and Oneata, Lau Group, Fiji Islands.

*Paratypes*.—Navutu-i-Loma: on ridge 150 yd. inland (Station 29, 1934) at 100 ft. elevation (28 specimens, BPBM 167103, ex BPBM 167020, ex BPBM 167055). Oneata: 1 mile north of Dakuiloa, ¼–1 mile inland (Station 99, 1938) at 25–50 ft. elevation (1 specimen, BPBM 180160).

*Remarks*.—The shell from Oneata (BPBM 180160) is juvenile, height 0.82 mm., diameter 1.81 mm., H/D ratio 0.455, whorls 3½, umbilicus 0.58 mm., D/U ratio 3.09, and may not belong to this species. It is closer to *S. navutuensis* than to any other Lau species.

Only four examples were adult, the remaining 24 being juvenile or broken. The secondary spiral cording is visible only under ideal angular lighting. It is widely spaced and distinctly more prominent than the radial microribbing.

### *Sinployea adposita* (Mousson, 1870). Figures 67g, 69d–f.

*Patula adposita* Mousson, 1870, J. de Conchyl., 18, pp. 119–120, pl. 7, fig. 8.—Oneata, Lau Group, Fiji Islands; Garrett, 1887a, Proc. Zool. Soc. London, 1887, p. 178.

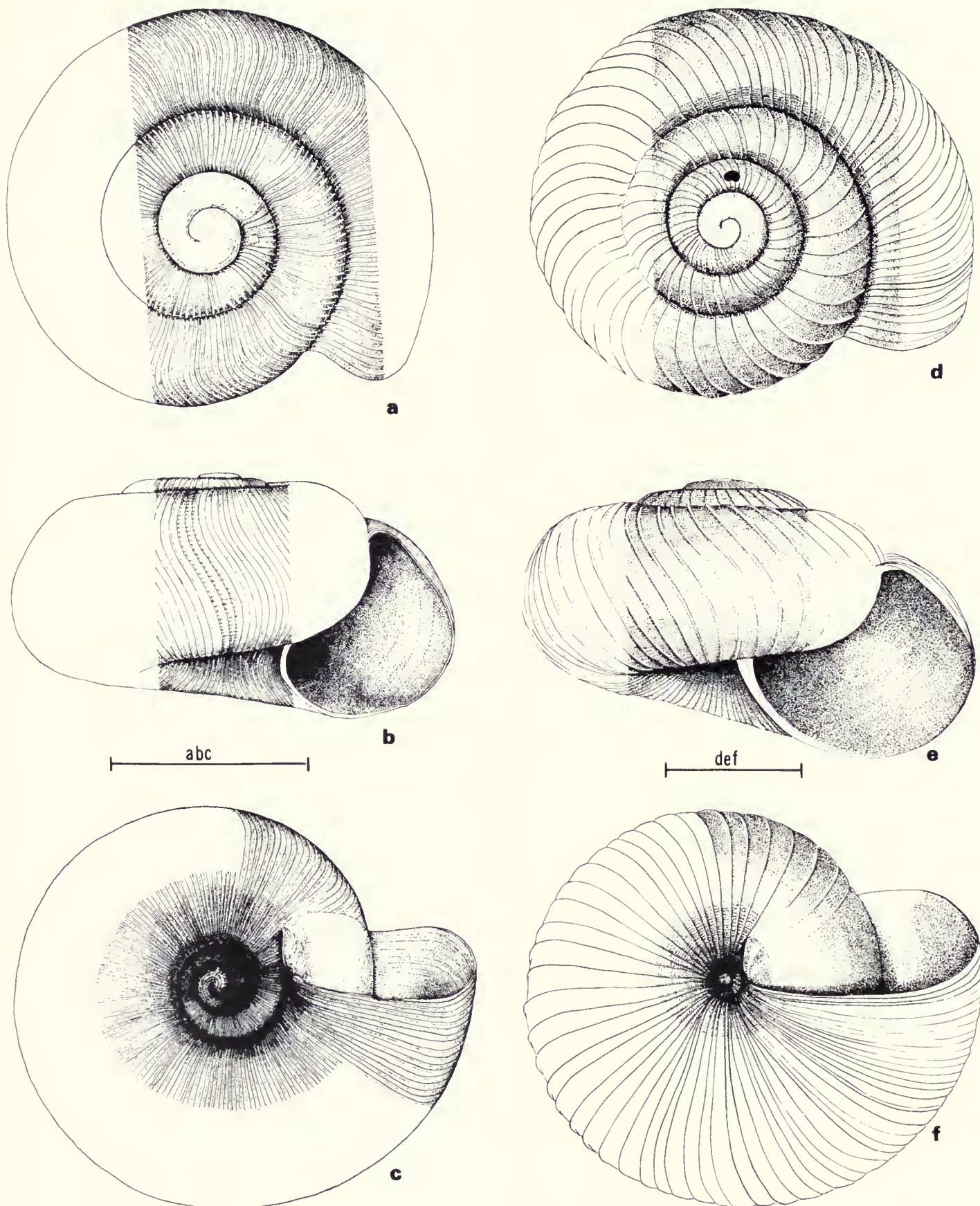


FIG. 69. a-c, *Sinployea godeffroyana*, new species. Station 133, Nandarivatu, 2,300-2,500 ft., Viti Levu, Fiji. Holotype. BPBM 179080; d-f, *Sinployea adposita* (Mousson). Station 100, Oneata, Lau, Fiji. BPBM 180177. Scale lines equal 1 mm. (a-c, MM; d-f, SH).



*Helix adposita* (Mousson), Pfeiffer, 1876, Monog. helic. viv., 7, p. 166.

*Helix (Patula) adposita* (Mousson), Tryon, 1887, Man. Conchol., (2) 3, p. 41, pl. 8, figs. 58–59.

*Endodonta (Charopa) adposita* (Mousson), Pilsbry, 1894, Man. Conchol., (2) 9, p. 35.

*Charopa adposita* (Mousson), Gude, 1913, Proc. Malacol. Soc. London, 10 (5), p. 330; Germain, 1932, Ann. Inst. Ocean., 12 (2), p. 45.

**Diagnosis.**—Shell large, diameter 2.63–3.75 mm. (mean 3.29 mm.), with 4–4½ rather tightly coiled whorls. Apex and spire moderately to strongly and evenly elevated, body whorl descending much more rapidly, spire protrusion about ⅓–¼ body whorl width, H/D ratio 0.538–0.713 (mean 0.603). Apical sculpture of 12–14 (mean 13.0) rather fine spiral cords. Postnuclear sculpture of narrow, fine, strongly protractively sinuated radial ribs, 36–74 (mean 53.3) on the body whorl, whose interstices are 3–6 times their width. Ribs/mm. 3.35–7.23 (mean 5.28). Microsculpture of extremely fine radial riblets, usually more than 10 between each pair of major ribs, crossed by barely visible spiral riblets. Secondary spiral cords much more prominent than microradials, interstices about 3–4 times their width. Umbilicus very narrow, U-shaped, not or only slightly decoiling, contained 7.87–17.0 times (mean 11.9) in the diameter, margins rounded. Whorls strongly and almost evenly rounded, very slightly compressed laterally above periphery and on basal margin, aperture ovate, inclined about 30° from shell axis.

*Sinployea adposita* differs from all other Fijian species in its very narrow umbilicus and presence of relatively regularly spaced, major radial ribbing. Other Fijian species of similar size have either widely open umbilici or if the umbilical range approaches that of *S. adposita*, they have lost the major radial ribbing (*S. recurva*, fig. 64b) or have an angulated periphery (*S. angularis*, fig. 64e).

**Description.**—Shell relatively large, with slightly less than 4½ moderately loosely coiled whorls. Apex and spire moderately and evenly elevated, last whorl not descending much more sharply, H/D ratio 0.622. Apical whorls 1½, sculpture of about 12 fine spiral ribs with a secondary sculpture of much smaller, more closely spaced radial riblets. Remaining whorls with thin, protractively sinuated radial ribs, 49 on the body whorl, whose interstices are about 3–5 times their width. Microsculpture a lattice of very fine radial ribs crossed by finer, much more crowded spiral riblets with a secondary sculpture of much more prominent, moderately closely spaced spiral cords. Sutures moderately deep, whorls strongly rounded above, very slightly flattened laterally above periphery. Umbilicus very narrow, U-shaped, not decoiling, contained 13.60 times in the diameter. Color light reddish horn, without darker flammulations. Aperture ovate, inclined about 20° from the shell axis. Height of lectotype 1.81 mm., diameter 2.91 mm.

**Lectotype.**—Fiji: Lau Group, Oneata. Collected by Dr. Graeffe. JDCP 5246.

**Range.**—Oneata, Munia, Lakemba, Aiwa, Mothe, Tuvutha, Karoni, Nayau, Yangasa Levu, Lau Group, Fiji Islands.

**Paratypes.**—Zurich, FMNH 116979, JDCP.

**Material.**—Oneata: southwest end of village (Station 100) ¼ mile inland at 100 ft. elevation (30 specimens, BPBM 180177–80). Lakemba (1 specimen, BPBM 180117; 30 specimens, AIM, FMNH, collected June 24–30, 1977, by Walter Cernohorsky): west end Tumba (Station 97) 10 ft. to ¼ mile inland at 15 ft. elevation (26 specimens, BPBM 180099–102). Munia: Hysik's plantation (Station 64), 50 yd. inland, 100–600

ft. elevation (1 specimen, BPBM 179294); northeast middle of island (Station 65), back of Hysik's home, ½ mile inland at 600–900 ft. elevation (5 specimens, BPBM 179322). Nayau: ¾ mile north of Liku Village (Station 101) 100 yd. inland at 30–500 ft. elevation (14 specimens, BPBM 180260); Nauko (Station 43) ½ mile inland at 250 ft. elevation (4 specimens, BPBM 167235). Yangasa Levu: south end Yangasa Levu (Station 30) 150 ft. elevation (67 specimens, BPBM 167140). Aiwa: Vataniyambia, southwest quarter of island (Station 40) 50 yd. inland at 25 ft. elevation (7 specimens, BPBM 167210). Karoni (100 specimens, AIM, FMNH, collected July 4, 1977, by Walter Cernohorsky): slope of peak at 90 ft. elevation (9 specimens, BPBM 78604–5); Mothe (1 specimen, AIM, collected July 7, 1977, by Walter Cernohorsky). Tuvutha: (Station F-7) west coast at 100 ft. elevation (6 specimens, FMNH 168132).

**Remarks.**—Specimens of *Sinployea adposita* show considerable variation in spacing of the major radial ribs and some variation in shell height. Mainly dead material in small sets was available.

Shells from Munia and the type set from Oneata (table XXXVII) are distinctly flatter with a lower H/D ratio than those from the remaining islands. Possibly there is subspeciation, but since most material was both dead and juvenile, such separation is premature.

Shells collected from Oneata Island in 1938 are unusual in having the radial ribbing extremely widely spaced, with 37–57 (mean 42.7) ribs on the body whorl. Those from Munia average 56 ribs on the body whorl; one unworn adult from Lakemba had 68; on Yangasa Levu they averaged 70.5; the single adult from Karoni Islet has 72; and on Nayau shells from two populations show the greatest extremes. Rib counts were not made on the 1977 collections from Lakemba and Karoni (Solem, 1978a). Specimens from ¾ mile north of Liku collected in 1938 have an average of 76.3 ribs on the body whorl, whereas the one adult collected at Nauko in 1934 has only 45 ribs, and the juveniles also have very widely spaced ribbing. This cannot be interpreted as meaning that the spacing of the ribbing necessarily varies seasonally since the two localities on Nayau yielded the quite distinct species *Vatusila kondoi* and *nayauana*. The variation in rib spacing shows no geographic pattern, and the populations show practically no variation in adult size (table XXXVII). The shells from Yangasa Levu, Mothe, and Munia have slightly narrower umbilici, but a minor size change produces a large numerical shift in this range of measurements.

**Description of soft parts.**—Fragmentary extracted individuals yielded partial genitalia and one pallial region. Latter typical, kidney 1.45 mm. in greatest length, rectal arm slightly longer than pericardial, arms of ureter widely separated by strip of lung roof.

Genitalia without unusual external features. Penis (fig. 67g, P) about 1.65 mm. long, internally with typical vergic papilla and small stimulatory pad.

TABLE XXXVII. - LOCAL VARIATION IN SINPLOYEA ADPOSITA AND S. IRREGULARIS.

	NUMBER OF SPECIMENS	RIBS	HEIGHT	DIAMETER	H/D RATIO
<u>adposita</u>					
Oneata Zurich	9	45.3±2.17 (36-54)	1.87±0.057 (1.62-2.09)	3.23±0.087 (2.95-3.64)	0.579±0.0080 (0.544-0.607)
Sta. 100, 1938 BPBM 180177-80	9	42.7±3.04 (37-57)	2.03±0.042 (1.85-2.22)	3.39±0.053 (3.11-3.64)	0.615±0.0080 (0.587-0.656)
Munia Sta. 64-5, 1938 BPBM 179322,-294	4	56.3±2.33 (52-60)	1.80±0.136 (1.56-2.12)	3.09±0.192 (2.72-3.51)	0.581±0.0105 (0.533-0.603)
Lakemba Sta. 97, 1938 BPBM 180099	3	-----	2.09±0.099 (1.89-2.19)	3.28±0.057 (3.18-3.38)	0.636±0.0329 (0.575-0.687)
Sta. 98, 1938 BPBM 180102,-17	6	68	2.09±0.045 (1.95-2.22)	3.42±0.084 (3.05-3.64)	0.613±0.0139 (0.574-0.650)
Yangasa Levu Sta. 30, 1934 BPBM 167140	5	70.5±0.50 (70-71)	1.97±0.036 (1.85-2.05)	3.21±0.053 (3.08-3.34)	0.614±0.0098 (0.594-0.649)
Nayau Sta. 101, 1938 BPBM 180260	4	76.3±6.18 (67-88)	1.90±0.109 (1.62-2.12)	3.27±0.092 (3.01-3.44)	0.581±0.0205 (0.538-0.616)
<u>irregularis</u>					
Zurich	7	-----	1.90±0.072 (1.71-2.20)	2.85±0.048 (2.67-3.08)	0.666±0.020 (0.613-0.764)
BPBM 7982	7	-----	1.79±0.058 (1.56-1.99)	2.78±0.041 (2.65-2.98)	0.643±0.014 (0.588-0.705)
Sta. 133, BPBM 179076,-9 2300- 2500'	18	-----	1.65±0.026 (1.51-1.91)	2.90±0.022 (2.70-3.09)	0.576±0.0091 (0.528-0.631)
Sta. 118, BPBM 178897 3000- 3600'	6	-----	1.71±0.043 (1.61-1.91)	2.97±0.030 (2.89-3.09)	0.575±0.0016 (0.544-0.617)
Sta. 139, BPBM 179157-8 2500- 2900'	2	-----	2.04±0.281 (1.76-2.32)	3.23±0.315 (2.91-3.54)	0.629±0.0262 (0.602-0.655)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>adposita</u>					
Oneata Zurich	4 1/4+(4-4 1/2)		0.27±0.012 (0.23-0.33)	12.2±0.56 (10.3-14.8)	-----
Sta. 100	4 1/2-(4 1/4-4 3/4)		0.30±0.021 (0.20-0.36)	11.4±0.78 (8.82-16.7)	13
Munia Sta. 64	4 3/8-(4-4 1/2)		0.24±0.043 (0.16-0.33)	13.8±1.72 (10.0-17.0)	-----
Lakemba Sta. 97	4 5/8+(4 1/2-4 7/8)		0.30	11.0±0.17 (10.7-11.3)	13
Sta. 98	4 1/2-(4 1/4-4 5/8)		0.36±0.031 (0.30-0.46)	9.64±0.66 (7.85-11.5)	-----
Yangasa Sta. 30	4 3/8-(4 1/8-4 1/2)		0.21±0.080 (0.20-0.23)	15.2±0.63 (13.3-16.8)	-----
Nayau Sta. 101	4 3/8-(4 1/4-4 1/2)		0.31±0.095 (0.30-0.33)	10.4±0.19 (10.1-11.0)	-----
<u>irregularis</u>					
Zurich	3 7/8-(3 5/8-4)		0.58±0.019 (0.49-0.66)	4.92±0.150 (4.35-5.36)	-----
BPBM 7982	3 5/8+(3 1/2-3 7/8)		0.58±0.021 (0.49-0.66)	4.76±0.159 (4.25-5.46)	18.0±1.16 (16-20)
Sta. Sta. 133	3 3/4+(3 5/8-4)		0.69±0.013 (0.59-0.79)	4.22±0.064 (3.79-4.77)	-----
Sta. 118	3 3/4-(3 1/4-4)		0.68±0.025 (0.59-0.76)	4.39±0.143 (4.13-4.88)	-----
Sta. 139	4 1/8(3 7/8-4 3/8)		0.81±0.116 (0.69-0.92)	4.01±0.184 (3.82-4.19)	-----



***Sinployea irregularis*** (Garrett, 1887). Figures 65d–f, 67a–d.

*Patula irregularis* Garrett, 1887, Proc. Zool. Soc. London, 1887, p. 179—Vitu Levu, Fiji Islands.

*Patula monstrosa* Ancey, 1889, Le Naturaliste, 1889, p. 71—Vitu Levu, Fiji Islands. New name for *irregularis* Garrett, 1887, not *Endodonta irregularis* Semper, 1874; Pilsbry, 1892, Man. Conch., (2) 8, p. 82.

*Endodonta (Charopa) monstrosa* (Ancey), Pilsbry, 1893, Man. Conch., (2) 9, p. 35. Listed *irregularis* Garrett, 1887, as a synonym, assuming it to be preoccupied by *Endodonta irregularis* Semper, 1874, now classified in *Aaadonta*.

*Charopa monstrosa* Ancey, Gude, 1913, Proc. Malacol. Soc. London, 10 (5), p. 330, pl. 14, figs. 6a, b, c; Germain, 1932, Ann. Inst. Ocean., 12 (2), p. 45.

**Diagnosis.**—Shell of average size, diameter 2.50–3.52 mm. (mean 2.87 mm.), with  $3\frac{3}{4}$ – $4\frac{3}{4}$  rather tightly coiled whorls. Apex and early spire flat to slightly elevated, lower spire descending moderately, body whorl often descending abruptly near aperture, spire protrusion variable, from  $\frac{1}{10}$ – $\frac{2}{5}$  (usually  $\frac{1}{5}$ ) body whorl width, H/D ratio 0.528–0.764 (mean 0.614). Apical sculpture of 16–20 (mean 18.5) fine, prominent spiral cords, becoming sinuated on crossing radial swellings. Postnuclear sculpture of highly variable, irregularly spaced, low to high, protractively sinuated radial ribs, rarely regular and persistent enough to count. Microsculpture of fine radial riblets, finer and more crowded spiral riblets, and rather prominent, widely spaced secondary spiral cords. Umbilicus relatively narrow, V-shaped, last whorl regularly to more rapidly decoiling, contained 3.79–6.83 times (mean 4.54) in the diameter, margins rounded. Whorls strongly rounded above and on outer margins, flattened to weakly channeled laterally above periphery. Aperture circular, inclination varying from  $10^\circ$  to  $30^\circ$  depending on rate of body whorl descension.

The flat spire, irregular ribbing, and often abrupt body whorl descension effectively separate typical examples of *Sinployea irregularis* from other Fijian species. *Sinployea inermis* (fig. 66a–e) is separable by its regular ribbing, lower apical cord count, and elevated spire. *Sinployea rudis* (fig. 47d–f) from Rarotonga, Cook Islands, is very similar in sculpture and whorl contour, but is much larger (mean diameter 4.04 mm.), with only 8–12 apical cords, and has the apex distinctly elevated. *Ba humbugi* (fig. 74a–c) has the apex strongly elevated, few and very prominent apical cords, and the umbilicus a lateral crack or closed.

**Description.**—Shell of average size, with  $3\frac{3}{4}$  moderately tightly coiled whorls. Apex and early spire flat, last whorl descending abruptly, H/D ratio 0.623. Apical whorls  $1\frac{1}{2}$ , sculpture of about 16 wavy, prominent spiral ribs, crossing low, broadly rounded radial ribs that are stronger on the last portion of apical whorls. Postapical sculpture of irregular, lamellate, protractively sinuated radial ribs, greatly reduced on body whorl. Microsculpture of fine, irregularly spaced, radial riblets, crossed by finer and more crowded spiral riblets, plus more prominent, equally spaced spiral cords. Sutures deep, whorls strongly rounded above, strongly flattened laterally above periphery. Umbilicus narrow, last whorl decoiling more rapidly, contained 4.25 times in the diameter. Color light yellow-brown, partially leached from shell. Aperture nearly circular, somewhat deflected and flattened above periphery with protruded umbilical lip. Height of lectotype 1.74 mm., diameter 2.80 mm.

**Lectotype.**—Fiji: Viti Levu, ex Garrett, Museum Godeffroy. BPBM 7982.

**Range.**—Interior of Viti Levu, Fiji.

**Paratypes.**—Zurich, FMNH 116977, BPBM 7982.

**Material.**—Viti Levu (22 specimens, BPBM 167434, FMNH 46376, FMNH 48996, FMNH 46439): Saganakoreva area back of Tubarua sawmill (Station VL-2, 1965), 5 miles in from Ngaloa, Nuku District, at 950–1,000 ft. elevation (4 specimens, FMNH 153599, FMNH 153611); Mt. Korobamba (Station 60), 2 miles in at 1,000–1,300 ft. elevation (2 specimens, BPBM 178759); Nandarivatu (Station 129), Nukunuku Creek, 12 miles inland at 2,000 ft. elevation (1 specimen, BPBM 179031); Nandarivatu (Station 134), 1 mile east of Vatuthere, 12 miles inland at 2,000 ft. elevation (1 specimen, BPBM 179085); Nandarivatu (Station 133), 2 miles east of Vatuthere, 14 miles inland at 2,300–2,500 ft. elevation (31 specimens, BPBM 179076–9); Navai (Station 139), 1 mile west of Nandarivatu, 16 miles inland at 2,500–2,900 ft. elevation (2 specimens, BPBM 179157–8); northwest of Nangaranambulata Mt. (Station 122), 10 miles inland at 2,700–3,200 ft. elevation (1 specimen, BPBM 178955); Nandarivatu (Station 118), 10 miles inland at 3,000–3,600 ft. elevation (7 specimens, BPBM 178897–8); 500 ft. ridge (Station F-12) near main highway, Yarawa, southeast region (12 specimens, FMNH 168309, FMNH 168311); near Tau Village (Station F-14), 2 miles inland at 500 ft. elevation (1 specimen, FMNH 168336); Nandarivatu (Station F-16), ridge slope at 2,500 ft. elevation (2 specimens, FMNH 168363, FMNH 168382). Ovalau: upper Totoga Creek (Station F-10), in from Levuka (6 specimens, FMNH 168240, FMNH 168250).

**Remarks.**—We do not know where on Viti Levu the original specimens, presumably collected by Dr. Graeffe, were obtained. The types have a high H/D ratio produced by very sharp descension of the last whorl or whorl and one-half. Shells nearest to these, but distinctly less elevated and with a wider umbilicus (table XXXVII), were obtained by members of the Lapham Expedition at 2,500–2,900 ft. elevation near Navai lumber camp on the slopes of Mt. Victoria (Station 139). Shells from the vicinity of Nandarivatu (Stations 118, 129, 133, 134) and northwest of Mt. Nangaranambulata (Station 122) are much less elevated (table XXXVII) and have the radial sculpture greatly reduced in size. Shells from Saganakoreva also have relatively low H/D ratios and wide umbilici. The importance of these variations is unknown. The two specimens from near the top of Mt. Korobamba (Station 60) are as flat as the Nandarivatu shells, but the radial ribs are slightly more prominent and regularly spaced with very high periostracal extensions. Much more material from the interior of Viti Levu is needed in order to access the range of variation in *S. irregularis*.

A single scalariform example, with the last third of the body whorl completely detached, was seen. It has not been included in the measured material.

**Description of soft parts.**—Foot and tail retracted in all available specimens, general appearance typical.

Body color light yellow-white, no darker markings.

Pallial region extending  $\frac{5}{8}$  whorl apically. Lung roof clear, without granulations. Kidney bilobed, maximum observed length 1.8

mm., rectal lobe distinctly longer than pericardial. Ureter typical, no lung roof visible between arms. Heart  $\frac{2}{3}$  length of pericardial kidney arm, lying parallel to hindgut.

Ovotestis typical, occupying  $\frac{1}{2}$  whorl above stomach apex, one clump of acini lying parallel to whorl sides. Hermaphroditic duct typical. Albumen gland (fig. 67a, GG), talon (GT), and carrefour (X) without unusual features (fig. 67b). Prostate (DG) and uterus (UT) typical.

Vas deferens (VD) very slender for entire length. Epiphallus (E) with head greatly swollen, tapering rapidly to a narrow neck entering penial head lateral to insertion of penial retractor (PR), which is very short and arises from diaphragm. Penis (P) with upper section enormously swollen, about 0.8–1 mm. long, basal shaft slightly shorter and very narrow. Internally (fig. 67c–d) with vergic papilla greatly enlarged, stimulatory pad greatly reduced in prominence. Atrium (Y) long and narrow.

Free oviduct (UV) wide, almost equal in diameter to penis. Spermatheca (S) with very slender shaft, until just before joining free oviduct, head elongately oval, slender. Vagina (V) tapering rapidly to atrium.

(Based on BPBM 178897, 4 fragmentary examples.)

### *Sinployea godeffroyana*, new species. Figure 69a–c.

**Diagnosis.**—Shell very small, diameter 1.95–2.32 mm. (mean 2.12 mm.), with  $3\frac{3}{4}$ –4 normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl descending slightly, spire protrusion about  $\frac{1}{2}$  body whorl width, H/D ratio 0.557–0.619 (mean 0.595). Apical whorls with 8–11 (mean 9.67) very fine spiral cords. Postnuclear sculpture of very fine, narrow, low, protractively sinuated radial ribs, 85–152 (mean 117.7) on the body whorl, whose interstices are 1–4 times their width. Ribs/mm. 20.99–38.03 (mean 28.36). Microsculpture of very fine radial riblets, 2–5 between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a secondary sculpture of low and rather crowded spiral cording. Umbilicus narrow, V-shaped, regularly decoiling, contained 4.11–6.30 times (mean 5.26) in the diameter, margins rounded. Whorl contours typical, strongly rounded above, flattened laterally above periphery and weakly flattened on basal margin, aperture inclined about  $10^\circ$  from shell axis.

Small size and very crowded radial ribbing distinguish *Sinployea godeffroyana* from other Fijian species. *Sinployea angularis* (fig. 64d–f) is similar in size but has less than 50 radial ribs, an angulated periphery, and markedly elevated spire.

**Description.**—Shell very small, with  $3\frac{3}{4}$  moderately loosely coiled whorls. Apex and spire only slightly elevated, last whorl barely descending, H/D ratio 0.557. Apical whorls  $1\frac{1}{2}$ , sculpture of 8 widely spaced, relatively low spiral ribs. Remaining whorls with low, rounded, crowded, protractively sinuated radial ribs, 152 on the body whorl, whose interstices are 1–2 times their width. Microsculpture of 2–5 radial riblets between each pair of major ribs, crossed by very low and inconspicuous crowded spiral ribs, with a secondary sculpture of narrow, widely spaced spiral cords. Sutures relatively shallow, whorls strongly rounded above, broadly flattened laterally above periphery and on base of shell. Umbilicus narrowly V-shaped, last whorl decoiling slightly more rapidly, contained 4.11 times in the diameter. Color light yellow-brown without darker flammulations. Aperture subquadrangular, flattened laterally above periphery and on basal margin, inclined about  $10^\circ$  from shell axis. Height of holotype 1.28 mm., diameter 2.30 mm.

**Holotype.**—Fiji: Viti Levu, Station 133, Nandarivatu, 2 miles east of Vatuthere at 2,300–2,500 ft. elevation. Collected in damp forest by Yoshio Kondo on September 9, 1938. BPBM 179080.

**Range.**—Viti Levu and satellite islands, Fiji.

**Paratypes.**—Viti Levu: Mt. Korobamba (Station 63), in dense forest at 1,000 ft. elevation (1 specimen,

BPBM 178794); Nangava Island (Station 151), off south coast of Viti Levu (1 specimen, BPBM 179256).

**Remarks.**—The three specimens associated here as *Sinployea godeffroyana* agree in general shape and form, but diverge somewhat in sculpture. The shell from Nangava Island (BPBM 179256) has the sculpture much more widely spaced, and the umbilicus is much narrower, with the last whorl less expanded. The single specimen from Mt. Korobamba (BPBM 178794) was injured several times during its growth. The narrower body whorl and umbilicus may be a result of repaired injuries rather than indicating specifically important differences.

Until more material is available I prefer to treat these as members of one species, although the Nangava Island shell may belong to a separate taxonomic entity.

### MELANESIAN *Sinployea*

Without dissection of the Solomon and Bismarck species, their classification in *Sinployea* rather than in the most generalized group of *Pilsbrycharopa* (see Solem, 1970a) will be somewhat arbitrary. In general appearance these species have more similarities to *Sinployea*, but either classification could be correct. I have taken this opportunity to provide expanded diagnoses of the Bismarck Archipelago *S. novopommerana* and *S. descendens*, plus new descriptions of *S. nissani* and *S. solomonensis*.

These species share monochrome coloration, rather tight coiling, wider than usual umbilici (except *S. solomonensis*), average ribbing, rather low H/D ratios, and are the smallest in average size for any area sampled (table XXXVIII). Only *S. solomonensis* and *S. euryomphala* even approach average size for the genus. The other four are among the seven smallest *Sinployea* species. Only the Fijian *S. angularis* and *S. godeffroyana* plus the Ellice Island *S. ellicensis nukulae-laeana* are slightly smaller.

Dissection of the penial complex in *S. euryomphala* confirmed my impression that *Sinployea* extends into the New Hebrides. Dissection of some *Andrefrancia* from New Caledonia (unpublished data) show that they are generically distinct. The only dissected *Pilsbrycharopa* from New Guinea is not one of the generalized species, so the closeness of relationship is uncertain.

Less detailed study has been made on this material, but a review is included here rather than making a separate report. Obviously collections are fragmentary and do not indicate actual distributions, but only the transitory passages of malacological collectors or friends of malacologists. Both Bismarck species came from river drift, although they may be sympatric. All three known Solomon Island species are allopatric, whereas the single New Hebridean species seems to be widely distributed in both the New Hebrides and Banks Group. Very probably, additional taxa will be



TABLE XXXVIII. — RANGE OF VARIATION IN MELANESIAN SINPLOYEA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<i>nissani</i> (De11)	1	87	12.85	1.00	2.15	0.466
<i>kuntzi</i> (Solem)	5	102.7(93–117)	15.0(13.64–16.18)	1.17(0.99–1.37)	2.18(2.06–2.30)	0.537(0.480–0.593)
<i>novopommerana</i> (Rensch)	38	92.7(67–105)	13.09(9.61–16.94)	1.18(0.99–1.61)	2.27(1.97–2.85)	0.519(0.467–0.567)
<i>descendens</i> (Rensch)	90	91.7(77–103)	12.93(11.13–14.65)	1.18(1.05–1.28)	2.27(2.14–2.53)	0.518(0.470–0.550)
<i>solomonensis</i> (Clapp)	1	89	10.31	1.38	2.75	0.503
<i>euryomphala</i> (Solem)	10	74(72–78)	9.43(8.93–9.94)	1.38(1.28–1.48)	2.64(2.43–2.93)	0.523(0.494–0.535)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW
<i>nissa.</i>	3 1/2	0.67	3.20	10	--	--	--
<i>kuntzi</i>	3 3/4(3 1/2–4)	0.56(0.51–0.61)	3.91(3.68–4.26)	11.5(11–12)	0.12(0.10–0.15)	0.63(0.56–0.71)	0.191(0.176–0.209)
<i>novop.</i>	3 3/4–(3 1/2–4 1/8)	0.65(0.53–0.92)	3.49(3.09–3.96)	10.8(10–12)	0.09(0.07–0.13)	0.69(0.61–0.76)	0.124(0.098–0.174)
<i>desce.</i>	4 1/2–(4–4 1/2)	0.83(0.74–0.95)	2.73(2.43–2.94)	10.6(9–14)	0.04(0.03–0.05)	0.82(0.79–0.86)	0.049(0.038–0.063)
<i>solom.</i>	4+	0.64	4.29	12	--	--	--
<i>euryo.</i>	3 3/4+(3 1/2–4)	0.67(0.59–0.82)	3.97(3.56–4.67)	12.0(11–13)	0.11(0.10–0.13)	0.74(0.63–0.82)	0.149(0.120–0.170)

recorded when more adequate collections have been made.

**Sinployea euryomphala** (Solem, 1959). Figures 67i–j, 70a–c.

*Mocella euryomphala* Solem, 1959, Fieldiana: Zoology, **43** (1), pp. 83–85, pl. 6, figs. 7–8 (radula and penis complex), pl. 31, figs. 1–5 (shell)—Brigstock Point, Espiritu Santo, New Hebrides; Solem, 1962, Bull. Brit. Mus. Nat. Hist., Zool., **9** (5), p. 226—Norovorovo, Maewo, and Gaua, Banks Group, New Hebrides; Solem, 1963, Verhandl. Naturf. Ges., Basel, **74** (2), p. 163—Malo Island off Espiritu Santo, New Hebrides.

**Range.**—Espiritu Santo, Maewo, Gaua, Vanua Lava, New Hebrides.

**Material.**—Espiritu Santo: Brigstock Point (4 specimens, MCZ 186828, FMNH 54906, FMNH 109493). Maewo (1 specimen, FMNH 109384). Vanua Lava (5 specimens, AIM, AMS).

**Remarks.**—Use of the New Zealand genus *Mocella* as a repository for this species was based on a desire to avoid description of a new genus on inadequate data. Dissection of *Mocella* (unpublished data) shows that it is not closely related.

Very few specimens have been seen from any single locality. I have not found any significant differences and doubt that any separation into local races has occurred. A description of the anatomy is presented below, but illustrations were prepared only for the penial complex (fig. 67i–j).

**Description of soft parts.**—Foot bluntly rounded anteriorly, slightly tapering and bluntly rounded posteriorly. Pedal grooves very high on foot, uniting over tail, suprapedal slightly weaker than pedal. No caudal foss, caudal horn, or middorsal groove. Foot sole

undivided and without corrugations. Slime network finely textured, rectangular.

Body color pale yellow in preservative, ommatophores black.

Mantle collar short, thick, edge tapering. Pneumostome masked by a very small anterior left mantle lobe. No other accessory lobes or shell laps. Anus opening above and slightly anterior to external ureteric pore, which leads into a narrow V-groove, the urinary chamber, passing through pneumostome and mantle collar.

Pallial region typical of subfamily. Kidney bilobed, rectal lobe  $\frac{1}{3}$  longer than pericardial and lapping onto hindgut. Ureter sigmoid, not expanded at any place, with strip of lung roof between arms. Hindgut continuing along parietal-palatal margin well apicad of pallial cavity. Heart elongated, slightly more than  $\frac{1}{2}$  length of pericardial kidney lobe. Lung roof clear, without color patches.

Ovotestis a single clump of finger-like acini buried in digestive gland well above stomach-intestine reflexion. Hermaphroditic duct an iridescent muscular tube, greenish in tone, narrowing at base of albumen gland, then running up to enter duct of talon at midpoint. Head of talon a white bulb, duct slender, opening directly into prostate-uterus head. Latter area torn in dissection, greatly distorted because of contraction, not worked out as to detailed structure.

Vas deferens a very slender tube passing up along lower half of penis, entering expanded tube of epiphallus above midpoint of penis. Epiphallus (fig. 67i, E) an expanded tube with clearly defined longitudinal pilasters, reflexed, with penial retractor (PR) inserting below point of reflexion (? artifact of contraction) and arising on diaphragm. Penis (P) showing two bulges externally. Apical portion with tiny verge (PV), the walls immediately below expanded to form a glandular collar (fig. 67j), lower part with a large glandular stimulatory papilla (PP) and a peculiar U-shaped pocket (PC) with thin muscular walls. Base of penis narrowing to atrium (Y) with weak pilasters present.

Free oviduct muscular, thick, with terminal glandular collar above junction with spermatheca. Latter with grossly expanded, thin-walled glandular base, narrowing to a very fine tube about midpoint of free oviduct. Position of spermathecal head not observed. Vagina very short and thin-walled.

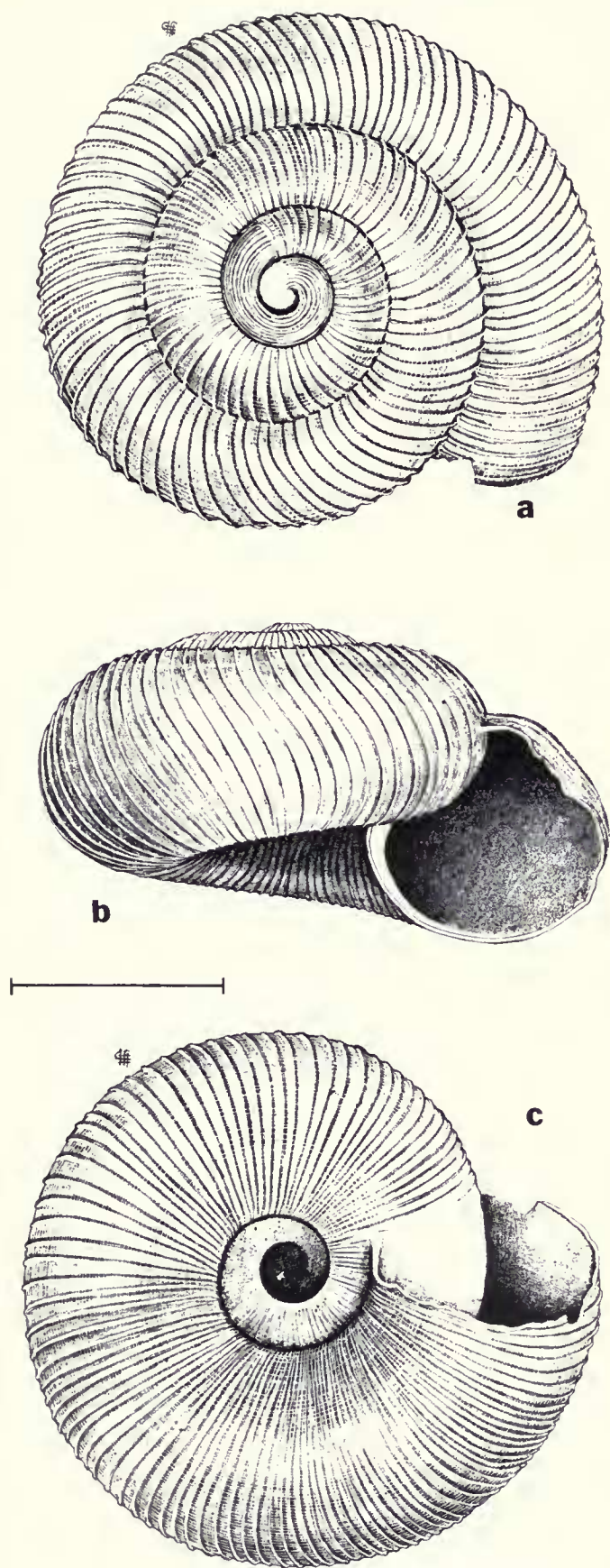


FIG. 70. a-c, *Sinployea euryomphala* (Solem). Holotype of *Mocella euryomphala* Solem. Under logs at Brigstock Point, Espiritu Santo, New Hebrides. UMMZ 186042. Scale line equals 1 mm. (Solem, 1959a, pl. 31, fig. 1-3). (EJP).

Digestive and free muscle system not studied. Buccal mass lost in dissection.

The single specimen available for dissection was retracted far within the shell and proved quite difficult to dissect. Destruction of the shell was mandatory, although the fragments have been saved. Diameter of the specimen was 2.27 mm. Radular elements of this species were figured previously (Solem, 1959a, pl. 6, fig. 7).

***Sinployea solomonensis* (Clapp, 1923). Figure 71a-e.**

*Endodonta (Charopa) solomonensis* Clapp, 1923, Bull. Mus. Comp. Zool., Harvard, 65, p. 378, figs. 21-24—Ugi, Solomon Islands.

*Mocella solomonensis* (Clapp), Solem, 1959, Fieldiana: Zoology, 43, p. 83; Solem, 1960, J. Malacol. Soc. Australia, 4, p. 41, pl. 4, figs. 1-5.

**Description.**—Shell of average size, with a little more than 4 normally coiled whorls. Apex and early spire slightly emergent, body whorl descending a little more rapidly, H/D ratio 0.503. Apical whorls 1%, sculpture of 12 rather small spiral cords. Postnuclear whorls with prominent, rounded, somewhat protractively sinuated radial ribs, 89 on the body whorl, whose interstices are 2-4 times their width. Ribs/mm. 10.31. Microsculpture mostly eroded, in places visible as a lattice of fine radial riblets crossed by even finer and more crowded spiral riblets. Sutures deep, whorls somewhat shouldered above, flattened laterally above periphery with slightly flattened basal margin. Color light reddish yellow-horn without darker markings. Umbilicus V-shaped, regularly decoiling, contained 4.29 times in the diameter. Aperture subcircular, slightly flattened laterally above periphery, inclined about 15° from the shell axis. No apertural barriers. Height of holotype 1.38 mm., diameter 2.75 mm.

**Holotype.**—Solomon Islands: Ugi Island. Collected by William Mann. MCZ 36838.

**Range.**—Ugi, Solomon Islands.

**Remarks.**—A proportionately thinner body whorl and slightly more crowded radial ribbing are the most obvious features separating this species from *Sinployea euryomphala*.

***Sinployea kuntzi* (Solem, 1960). Figure 72a-c.**

*Mocella kuntzi* Solem, 1960, J. Malacol. Soc. Australia, 4, pp. 41-42, pl. 5, A, figs. 1-3—Station FLW 38, peninsula east of Halavo, Florida Island, Solomon Islands.

**Range.**—Florida Island, Solomon Islands.

**Material.**—Florida Island: peninsula east of Halavo (5 specimens, FMNH 54905, MCZ 186827).

**Remarks.**—Data on variation are presented in Solem (1960). Measurements in Table XXXVIII are based upon material measured recently and thus differ slightly from the data recorded in the original description. Differences from *S. nissani* are covered in the remarks under that species.

***Sinployea nissani* (Dell, 1955).**

*Gyropena nissani* Dell, 1955, Pacific Science, 9, p. 328, fig. 1, e-g—near Tangalan Plantation, Nissan Id., Northern Solomons.

*Mocella nissani* (Dell), Solem, 1960, J. Malacol. Soc. Australia, 4, pp. 41, 43.

**Description.**—Shell very small, with 3½ moderately loosely coiled whorls. Apex barely emergent, spire flat, last whorl not descending, H/D ratio 0.466. Apical whorls 1%, sculpture partially eroded with traces of about 10 relatively widely spaced spiral cords remaining. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, 87 on the body whorl, whose interstices



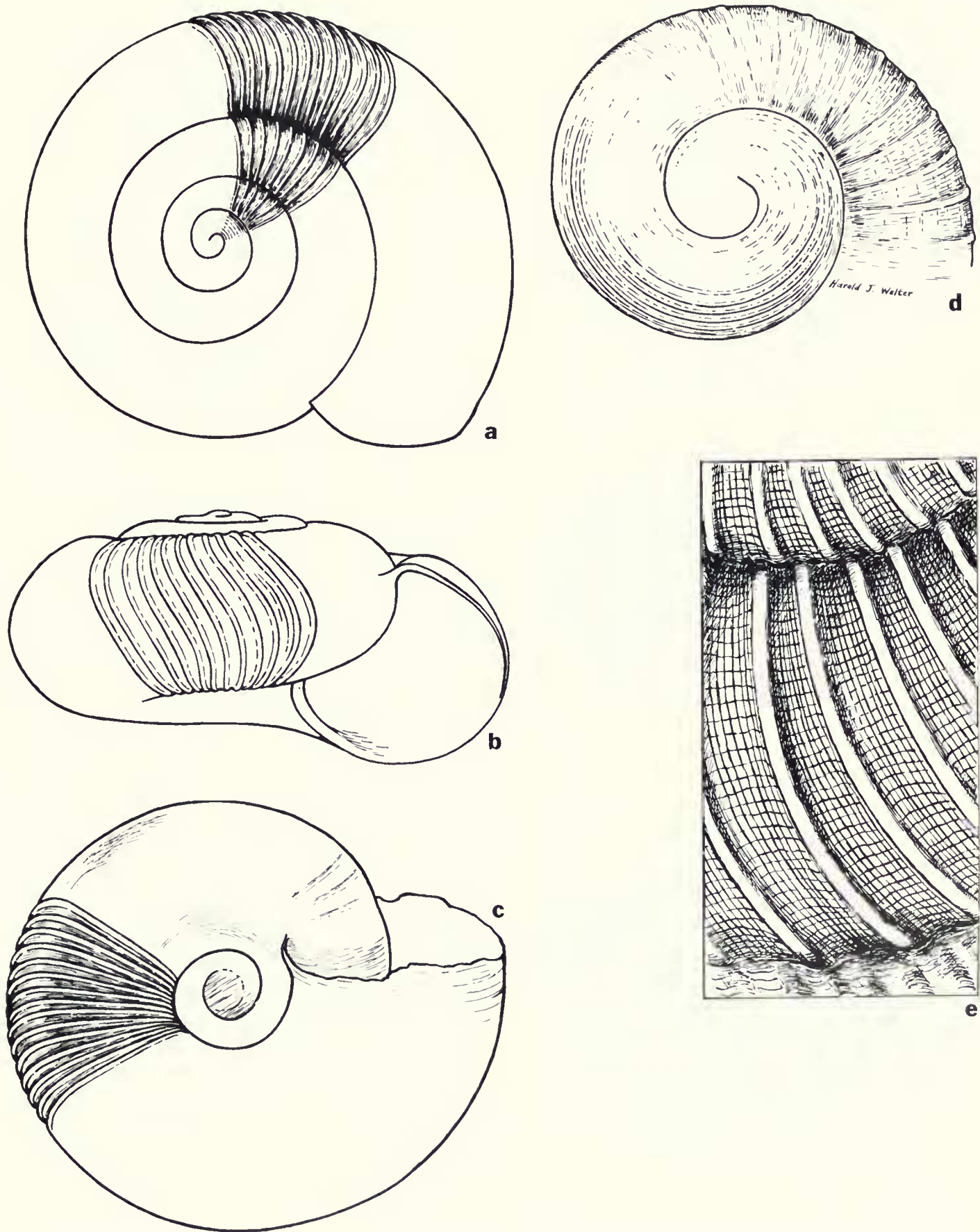


FIG. 71. *Sinployea solomonensis* (Clapp). Holotype of *Charopa solomonensis* Clapp. Ugi Island, Solomon Islands. MCZ 36838: a-c, entire shell; d, detail of partly worn apical sculpture, greatly enlarged; e, detail of microsculpture, greatly enlarged, absence from tops of major ribs caused by mechanical wear. Scale line equals 1 mm. (Solem, 1960, p. 42, pl. 4). (HJW).

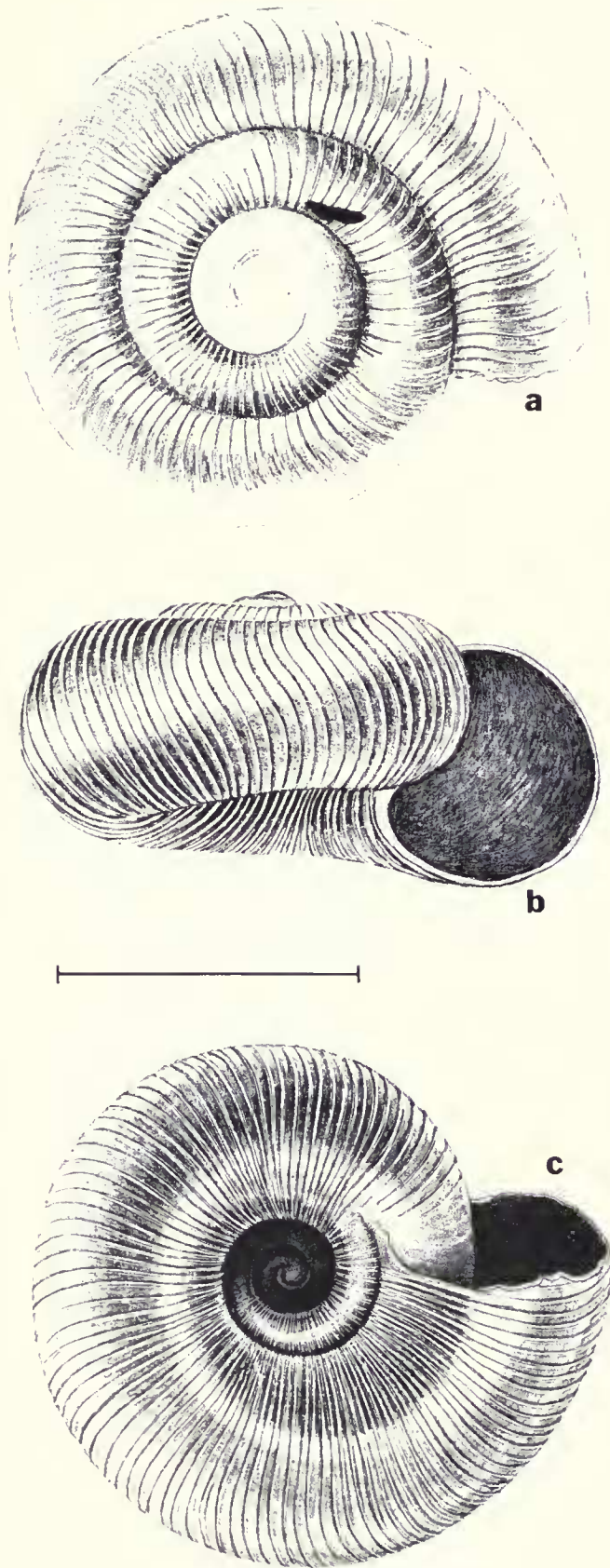


FIG. 72. a-c, *Sinployea kuntzi* (Solem). Holotype of *Mocella kuntzi* Solem. From jungle one mile behind Halavo, Florida Island, Solomon Islands. UMMZ 184473. Scale line equals 1 mm. (Solem, 1960, p. 44, pl. 5, fig. A). (EJP).

are 2-4 times their width. Ribs/mm. 12.85. Microsculpture of fine radial riblets, 4-7 between each pair of major ribs, with much finer, more crowded spiral riblets and a relatively prominent secondary sculpture of widely spaced spiral cording. Sutures deep, whorls evenly rounded above, slightly flattened laterally above periphery with gently rounded basal margin. Color uniform yellowish brown, slightly faded. Umbilicus widely open, broadly U-shaped, regularly decoiling, contained 3.20 times in the diameter. Aperture ovate, lip badly broken. Height of holotype 1.01 mm., diameter 2.16 mm.

**Holotype.**—Solomon Islands: Nissan Island, near Tangalan Plantation. Collected in leaf mould by R. K. Dell in June, 1944. DMW 2513.

**Range.**—Nissan Island, Solomon Islands.

**Remarks.**—As indicated by Solem (1960), *Sinployea nissani* is quite closely related to *M. kuntzi* from Florida Island. The latter is a distinctly higher shell (mean height 1.17 mm.), with much narrower umbilicus (mean D/U ratio 3.91). Even though the type of *S. nissani* is subadult, the umbilical width is greater than in *S. kuntzi*. Although adult descension of the last part of the body whorl would have increased the H/D ratio of *S. nissani*, presumably the more rapid decoiling of the last umbilical section would have further widened the umbilical opening, increasing the difference. They are distinct species.

***Sinployea novopommerana*** (I. Rensch, 1937). Figure 73a-c.

*Charopa novopommerana* I. Rensch, 1937, Arch. f. Naturgesch., n.f., 6 (4), pp. 589-590, figs. 33-34 (shell and radular teeth)—Karlei, Malkong-Bach, and Nangurup, New Britain, Bismarck Archipelago.

**Diagnosis.**—Shell very small, diameter 1.97-2.85 mm. (mean 2.27 mm.), with  $3\frac{1}{2}$ -4 $\frac{1}{2}$  normally coiled whorls. Apex and early spire slightly elevated, rounded above, body whorl descending much more rapidly, spire protrusion about  $\frac{1}{8}$  body whorl width, H/D ratio 0.467-0.567 (mean 0.519). Apical sculpture of 10-12 (mean 10.8) very fine spiral cords. Postnuclear whorls with prominent, rounded, protractively sinuated radial ribs, 67-105 (mean 92.7) on the body whorl, whose interstices are 2-4 times their width. Ribs/mm. 9.61-16.94 (mean 13.09). Microsculpture of fine radial riblets, 5-10 between each pair of major ribs, slightly finer and more crowded spiral riblets, plus rather crowded secondary spiral cording that is slightly more prominent than microradials. Umbilicus moderately open, V-shaped, last whorl decoiling more rapidly, contained 3.09-3.96 times (mean 3.49) in the diameter, margins rounded. Sutures very deep, whorls strongly rounded above, flattened laterally above rounded periphery, with evenly rounded, slightly compressed, basal margin. Color light reddish yellow-horn without darker flammulations. Aperture subcircular, flattened laterally above periphery, inclined about 30° from shell axis.

*Sinployea novopommerana* has a much less compressed body whorl and narrower umbilicus than *S. descendens* (fig. 73d-f). *Sinployea kuntzi* has a much more elevated spire, narrower umbilicus, and less marked lateral flattening above the periphery (fig. 72a-c).

**Range.**—New Britain, Bismarck Archipelago.

**Material.**—New Britain: Karlei (34 specimens, ZMB, FMNH 146028); Malkong (4 specimens, ZMB).

**Remarks.**—The slightly elevated apex and rather narrow and V-shaped umbilicus immediately separate



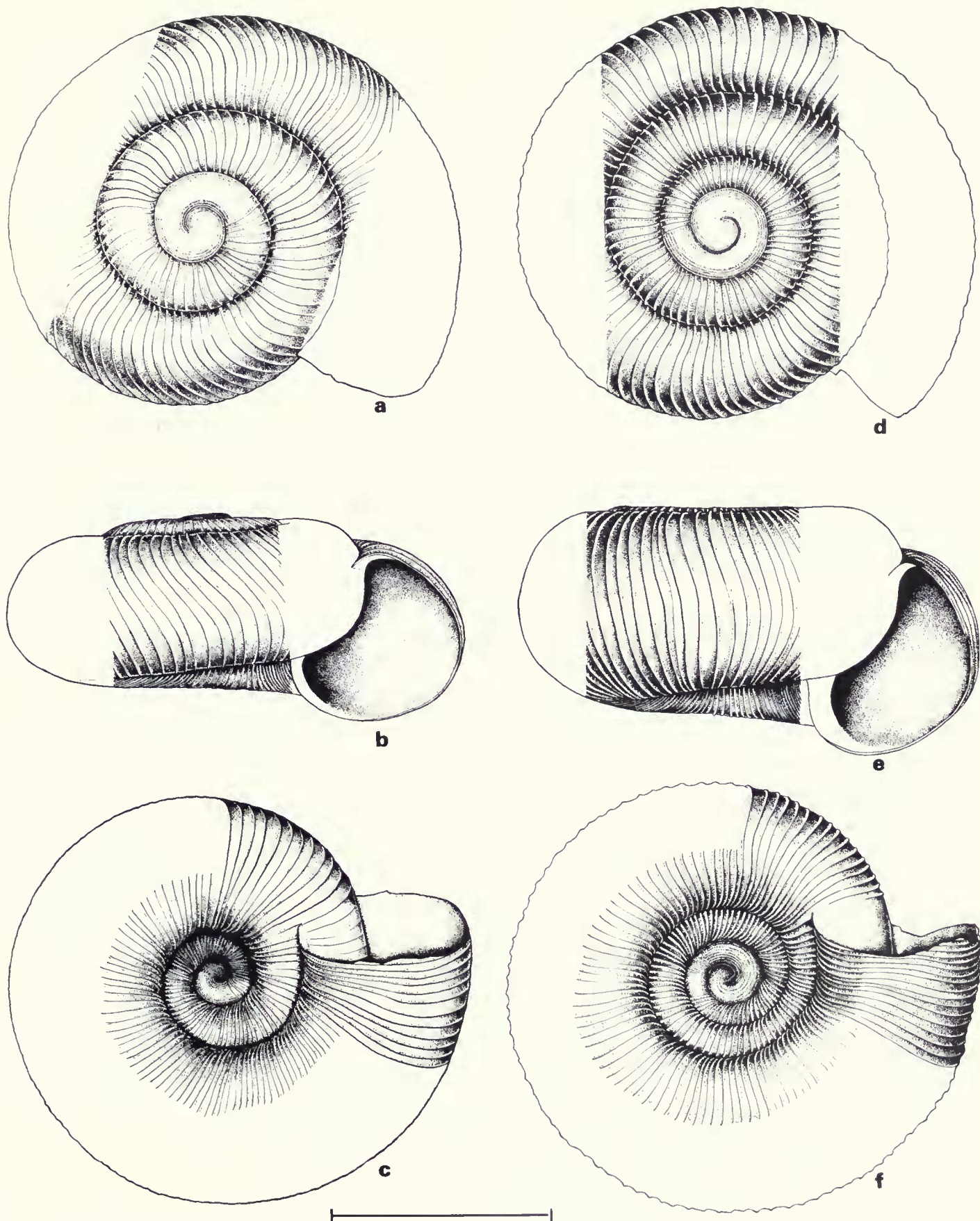


FIG. 73. a-c, *Sinployea novopommerana* (Rensch). Karlei, Weite Bucht, New Britain, Bismarck Archipelago. Paratype. FMNH 146028; d-f, *Sinployea descendens* (Rensch). Karlei, Weite Bucht, New Britain, Bismarck Archipelago. Paratype. FMNH 146029. Scale line equals 1 mm. (MM).

*Sinployea novopommerana* (fig. 73a-c) from the sympatric *S. descendens* (fig. 73d-f). The Solomon Island *S. solomonensis* (Clapp, 1923) appears quite similar but is larger, has a slightly narrower umbilicus, the whorls are less flattened laterally above the periphery, and the whorl count is slightly higher (fig. 71a-e). *Sinployea nissani* (Dell, 1955) and *S. kuntzi* (Solem, 1958) are smaller, much more tightly coiled shells.

Most of the available specimens were not quite fully adult, so that the mean diameter recorded in the diagnosis may be too small. The range is greatly extended in regard to height, diameter, and umbilical width by the presence of one very large individual. Without this specimen, the maximum height would be 1.33 mm., maximum diameter 2.47 mm., and maximum umbilical width 0.74 mm. If this specimen is a freak, there would be a more marked size differential between *S. novopommerana* and *S. euryomphala*.

***Sinployea descendens* (I. Rensch, 1937). Figure 73d-f.**

*Charopa descendens* I. Rensch, 1937, Arch. f. Naturgesch., n. f., 6 (4), p. 590, fig. 35—Karlei, Malkong, and Matong, New Britain, Bismarck Archipelago.

**Diagnosis.**—Shell very small, diameter 2.14–2.53 mm. (mean 2.27 mm.), with 4–4½ rather tightly coiled whorls. Apex and early spire flat or slightly depressed below level of penultimate and first half of body whorl, last half of body whorl descending markedly, total spire protrusion about ½ of body whorl width, H/D ratio 0.470–0.550 (mean 0.518). Apical sculpture of 9–14 (mean 10.6) prominent, regularly spaced spiral cords, whose interstices are less than twice their width. Postnuclear sculpture of prominent, high, rounded, rather crowded, slightly protractively sinuated radial ribs, 77–103 (mean 91.7) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 11.13–14.95 (mean 12.93). Microsculpture of fine radial riblets, 5–8 between each pair of major ribs, finer spiral riblets, and narrow, quite crowded, secondary spiral cords. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.43–2.94 times (mean 2.73) in the diameter, margins slightly shouldered. Sutures deep, whorls shouldered above and on basal margin, evenly rounded on columellar margin, strongly compressed laterally above rounded periphery. Color reddish horn fading to yellow-white in drift material, no flammulations. Aperture suboval, sharply rounded above and at basal margin, evenly rounded laterally, inclined about 10° from shell axis.

*Sinployea descendens* is characterized by its flat spire, widely open cup-shaped umbilicus, and thick body whorl. The sympatric *S. novopommerana* (fig. 73a-c) has a much narrower umbilicus, thinner body whorl, distinctly elevated spire, and averages ½ whorl less at identical size. *Sinployea irregularis* (fig. 65d-f) from Fiji is very similar in appearance, but is much larger, has reduced ribbing, and a narrow umbilicus.

**Range.**—New Britain, Bismarck Archipelago.

**Material.**—New Britain: Karlei (76 specimens, ZMB, FMNH 146029); Matong (14 specimens, ZMB).

**Remarks.**—Both *Sinployea nissani* and *S. kuntzi* are more narrowly umbilicated, have a protruding spire, and average one-half whorl less. Size variation in the two samples is summarized in Table XXXVIII. These were all drift specimens and undoubtedly originated from several populations.

**Genus *Ba*, new genus**

Shell of less than average size with only 3¼–3½ tightly coiled whorls. Apex and spire quite elevated, body whorl descending rapidly. Apical sculpture of about 12 very prominent spiral cords. Postnuclear sculpture reduced to irregularity. Umbilicus closed or barely open. Aperture without barriers. Pallial region with markedly deflected hindgut and kidney, latter squarish with tightly compacted ureter arms. Ovotestis with one acinal clump, hermaphroditic duct short. Prostate-uterine region folded and compacted. Penis with unusually complicated penial retractor insertion. Interior of penis with large vergic papilla and circular muscle band, pocket stimulator greatly reduced in size.

**Type species.**—*Ba humbugi*, new species.

In pattern of sculpture and general appearance, *Ba humbugi* is extremely similar to the sympatric *Sinployea irregularis* (Garrett). The major conchological differences are the extreme spire elevation, marked whorl reduction, and umbilical closure of *Ba humbugi*. Anatomically, the compaction and deflection of the kidney and hindgut (fig. 75a) represent a major departure from the Charopidae pattern. Similar whorl reduction in the Caroline Island *Russatus* (fig. 90a) required only compaction into a square kidney without deflection of either kidney or hindgut from the parietal-palatal margin. The New Guinea endemic *Paryphantopsis* (Solem, 1970a, p. 250, fig. 2, a) agrees with *Ba* in showing kidney and hindgut deflection, but the pattern of the kidney is quite different in that the ureter arms become spread progressively further apart. These are different solutions to the same problem of visceral hump compaction. Also part of this problem is the alteration in penial retractor muscle insertion.

The functioning penial surface structures of *Ba humbugi* show simple character displacement from the equivalent structures in *Sinployea irregularis*, thus indicating phyletic closeness. Yet *Ba humbugi* is the only known member of the Pacific Island Charopinae to experiment with whorl reduction and visceral hump compaction. Because it represents a basic departure from the *Sinployea* pattern, I have chosen to give generic level recognition despite its evident relationships to *S. irregularis*.

The only known species, *Ba humbugi*, has been found in Central Viti Levu from Mt. Nangaranambulata south to a few miles inland from Ngaloa. At the latter locality it was found under the same log as *Sinployea irregularis*. Because it occupies a portion of Viti Levu that includes the Mba District, I have chosen the European spelling of the district for a generic name. This was followed by an irresistible impulse to use the specific name *humbugi*.

***Ba humbugi*, new species. Figures 74a-c, 75a-h.**

**Diagnosis.**—Shell of slightly less than average size, diameter 2.30–3.32 mm. (mean 2.72 mm.), with 3¼–3½ tightly coiled whorls. Apex and spire strongly and evenly elevated, body whorl descending more rapidly, spire protrusion ⅓–½ body whorl width, H/D ratio 0.752–0.842 (mean 0.801). Apical sculpture of 11–13 (mean 12.0) high and prominent spiral cords. Postnuclear sculpture of irregular growth wrinkles and an occasional identifiable major rib with inter-



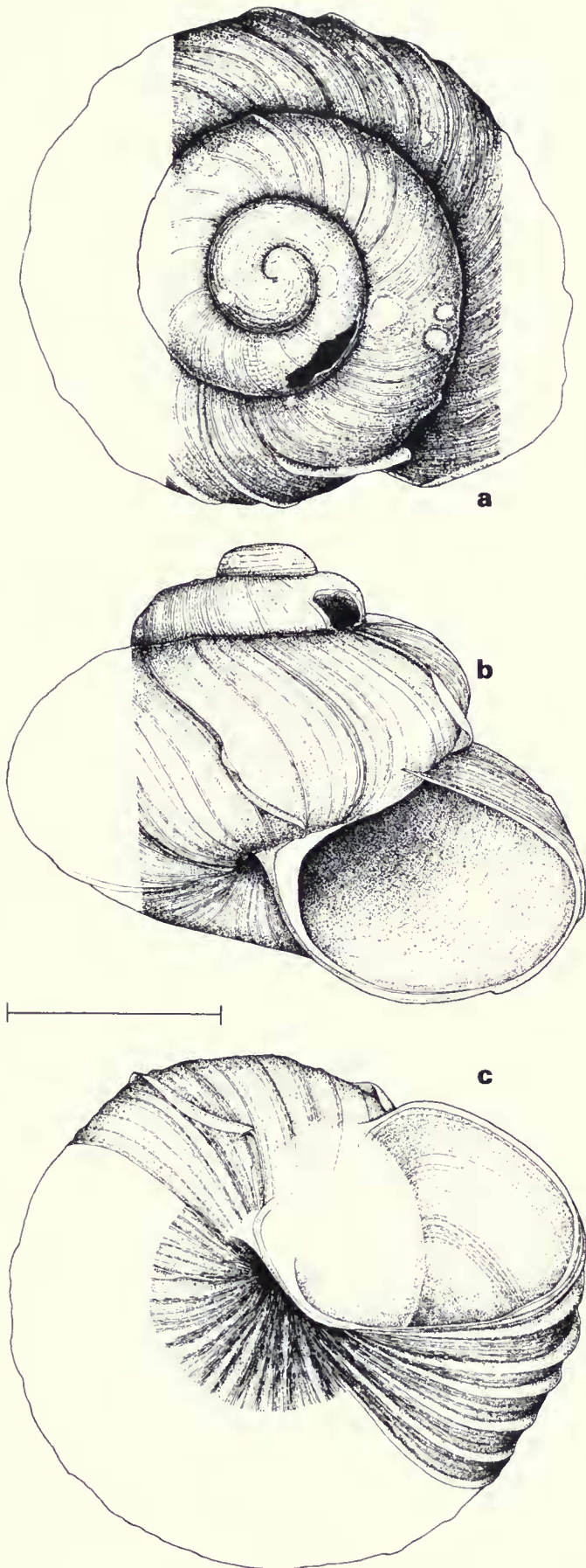


FIG. 74. a-c, *Ba humbugi*, new species. Mt. Nangaranambulata, 2,700–3,200 ft., Viti Levu, Fiji. Holotype. BPBM 178954. Scale line equals 1 mm. (MM).

gradation between these extremes. Microsculpture obscured by surface irregularities, visible in some areas as consisting of fine radial riblets, finer and more crowded spiral riblets, plus low and broadly rounded, much larger secondary spiral cords. Umbilicus either imperforate (25%) or with a small lateral crack (75%), possibly latter developing in adult stage only, since smallest example had closed umbilicus. Sutures deep except near end of body whorl, aperture and body whorl flattened laterally above periphery, inclined about 25° from shell axis.

*Ba humbugi* is immediately recognizable by its very high spire, low whorl count, reduced radial ribbing, and closed or laterally cracked umbilicus. Other Polynesian species with closed or nearly closed umbilici include the Samoan *S. clausa* and *S. clista* (fig. 51c, f) and the Lau Archipelago *S. adposita* (fig. 69f). These species all have prominent radial ribbing and higher whorl counts. The Lord Howe Island *Mystivagor mastersi* (Brazier, 1872) is similar in shape and whorl count but has vastly different sculpture and anatomy.

*Description*.—Shell rather small, with  $3\frac{1}{2}$  relatively tightly coiled whorls. Apex and spire markedly and evenly elevated, body whorl descending more rapidly, H/D ratio 0.810. Apical whorls  $1\frac{1}{2}$ , sculpture of 11 very prominent spiral cords. Postnuclear whorls with very irregular growth wrinkles and occasional major ribs with high periostracal extensions. Microsculpture a lattice of fine radial and finer spiral riblets, irregular in spacing, crossed by more prominent spiral cords. Sutures deep, whorls flatly rounded above, evenly rounded below periphery. Umbilicus closed by expansion of basal lip and tight coiling, with only a slight lateral chink visible. Color light reddish yellow with dark brown, almost black, periostracal extensions. Aperture ovate, flattened laterally above periphery, inclined about 25° from shell axis. Height of holotype 2.24 mm., diameter 2.76 mm.

*Holotype*.—Fiji: Viti Levu, Station 122, Mt. Nangaranambulata at 2,700–3,200 ft. elevation. Collected in dense forest by Yoshio Kondo on September 5, 1938. BPBM 178954.

*Range*.—Interior of Viti Levu at 950–3,200 ft. elevation, Fiji.

*Paratypes*.—Viti Levu: top of Mt. Korobamba (Station 60) at 1,000–1,300 ft. elevation (2 specimens, BPBM 178758); Saganakoreva area (Station VL-2, 1965), back of Tubarua saw mill, 950–1,000 ft. elevation, 5 miles inland from Ngaloa, Nuku District (1 specimen, FMNH 153605).

*Remarks*.—The closed umbilicus, irregular ribbing, and very high spire of *Ba humbugi* immediately separate it from any Pacific Island endodontid. In many respects, the shell recalls that of the New Caledonian *Rhytidopsis minutula* (Crosse, 1870) (see Solem, 1961, p. 466). Until the latter can be dissected, the degree of relationship will remain uncertain. The Lord Howe Island species *Mystivagor mastersi* (Brazier, 1872) has gone further toward a succineiform shell. It differs in size (6 mm. diameter), strong color pattern, smooth shell surface, and apical sculpture of widely spaced radial ribs.

Spire angle varied greatly among the four specimens, with the one from Saganakoreva (FMNH 153605) having a much wider angle and lower H/D ratio (0.752). It was found under the same log as an example of *Sinployea irregularis*, so that the two

species are unquestionably sympatric. Lack of any black markings on the body probably indicates this is a strictly terrestrial species.

Dissection of two individuals showed major changes in the pallial systems that resulted in generic recognition. Changes in the genitalia involved folding of the prostate-uterus, compaction and broadening of the albumen gland, shortening of the hermaphroditic duct, altering the simple clump insertion of the penial retractor into a complex (fig. 75d-e), enfolding of the penis-epiphallus junction, and massive reduction of the penial pocket stimulator (fig. 75h). Except for the latter change, these are adjustments to the whorl reduction and visceral hump compaction.

Comparison of penial structures in *S. irregularis* (fig. 67c-d) with those of *Ba humbugi* (fig. 75h) shows enlargement of the pocket stimulator in the first and reduction in the second.

A single sperm packet (fig. 75f-g) was taken from FMNH 153605, which was collected December 9, 1965, the morning after a shower ending a long drought.

*Description of soft parts.*—Foot and tail equal in length to shell diameter. Sole undivided, bluntly rounded and slightly tapering posteriorly, truncated anteriorly. Pedal grooves very conspicuous, high on foot, uniting above tail, no caudal horn or middorsal groove developed. Slime network of large, rectangular sections on tail and sides of foot. Head retracted in all individuals examined. Gonopore position normal.

Body color yellow-white, no darker markings.

Mantle collar (MC) with thickened edge, no glandular extension onto pallial roof. Anus (A) opening next to external ureteric pore (KX), just inside pneumostome.

Pallial region (fig. 75a) extending  $\frac{1}{2}$  whorl apically. Lung roof clear, without granulations. Kidney (K) about 1.58 mm. long, bilobed, deflected downward from parietal-palatal margin after 0.33 mm., lobes subequal, pericardial slightly longer than rectal, truncated anteriorly by ureter. Ureter (KD) compressed between kidney lobes, apical part curved downward around tip of kidney, no lung surface visible between kidney lobes. Heart (H)  $\frac{2}{3}$  length of kidney, lying parallel to deflected plane of hindgut and parallel to lower edge of mantle collar. Principal pulmonary vein (HV) very short and inconspicuous, curving around edge of kidney. Hindgut (HG) deflected from parietal-palatal margin shortly after kidney apex, intestinal loop (dotted line in fig. 75a) partly under heart.

Ovotestis (fig. 75c, G) occupying  $\frac{1}{3}$  whorl above stomach apex, a single, tightly compacted clump of palmately clavate acini with short collecting tubule. Hermaphroditic duct (GD) kinked initially, narrow, gradually tapering to past middle, grossly expanded, then sharply constricting before reflexing up to talon. Albumen gland (GG) with highly irregular surface, proportionately large, acini relatively small. Talon (GT) with globular head, short neck to carrefour, both buried in albumen gland. Prostate (DG) with a few long acini inserting onto side of uterus, which is bifoliated. Uterus (UT) bipartite, folded upon itself, lower chamber enlarged and with thick, glandular walls.

Vas deferens (VD) with thick, glandular walls to penioviducal angle, narrowed abruptly and a thin-walled tube to epiphallus, loosely bound to penioviducal angle. Epiphallus (E)  $\frac{2}{3}$  length of penis, head bulbous, internally with Y valve and longitudinal pilasters. Folded against head of penis at point of insertion. Penial retractor (PR) arising from diaphragm, about  $\frac{1}{3}$  length of penis, inserting in a broad fan around epiphallus and head of penis (fig. 75d-e), with separate strands to penis apex and inner wall of epiphallus. Penis (P) club-shaped, about 1.8 mm. long, tapering gradually to atrium, internally (fig. 75h) with a bulbous vergic papilla, greatly enlarged circular muscle band, and tiny stimulatory pocket pilaster. Lower

portion with weak glandular ridges into atrium. Atrium (Y) short, without unusual features.

Free oviduct (UV) only slightly longer than vagina, equal in diameter to penis at midsection, internally with typical circular pilaster at spermathecal junction. Spermatheca (S) with expanded head next to albumen gland, slender shaft next to prostate, base section abruptly expanding at base of uterus, internally with typical glandular pilaster and a larger sperm packet (fig. 75f-g, SP). Vagina (V) thin-walled, same diameter as free oviduct, internally with weak glandular pilasters.

Free muscle system typical, somewhat shortened. Right omatophoral retractor passing through penioviducal angle, right rhinophoral retractor uniting before tail fan junction.

Stomach occupying  $\frac{7}{8}$  of a whorl, starting  $\frac{1}{16}$  of a whorl above pallial cavity apex. Intestinal looping compacted into narrow zone and protruding partly into pallial cavity area. Hindgut deflected from parietal-palatal margin for half of length, reaching margin near anterior end of kidney.

Digestive glands extending past ovotestis to apex, mainly along stomach, only one strand near albumen gland. Salivary glands short, not uniting above esophagus.

(Based on FMNH 153605 and BPBM 178954, 2 adult specimens.)

### Genus *Maafu*, new genus

Shell relatively large, with 4-4½ normally coiled whorls. Apex and spire flatly coiled, depressed below level of postnuclear sub-sutural keel. Periphery strongly protruded into a cordlike keel with prominent supra- and subperipheral sulci. Umbilicus broadly open, cup-shaped, regularly decoiling, contained about 3 times in the diameter. Apical sculpture with typical spiral cords. Postnuclear sculpture with prominent, widely spaced radial ribs that are enlarged on crossing periphery, regular microsculpture reduced, secondary spiral cording narrow, rather prominent, and quite crowded. No apertural barriers. Anatomy unknown.

*Type species.*—*Maafu thaumasius*, new species.

Although the form of *Maafu thaumasius* is partially duplicated by such Endodontidae as *Austral-donta magnasulcata* (Solem, 1976b, p. 295, fig. 127a-b), several *Nesodiscus*, *Endodonta*, and many juvenile *Gambiodonta*, no Pacific Island Charopidae have a protruded keel. Only *Sinployea angularis* (fig. 64e) from Namuka, Lau Group, and *Himeroconcha* (fig. 105b, e) from the Marianas have an angulated periphery.

Most of the greatly altered appearance seen in *Maafu thaumasius* relates to the two keels. The sub-sutural keel changes what would be a flat-spined shell into one that has a depressed apex and early spire. The extreme protrusion of the peripheral keel increases the diameter and decreases the H/D ratio. Hence, the comparatively large size (mean diameter 3.49 mm.) and very low H/D ratio (mean 0.365) are secondary modifications resulting from the keels. Efforts to assess the relationships of *M. thaumasius* must discount the importance of these size and shape shifts. The microsculpture of *Sinployea inermis meridionalis* and *S. i. lakembana* is visually very close to that of *M. thaumasius*. Only the greater crowding and emphasis of the secondary spiral cording distinguish the latter in a gross sense. The pattern of coiling, umbilical shape, and major ribbing is very different, but derivation of *Maafu* from the generalized *Sinployea inermis*-*S. princei* stock would present no insuperable difficulties.



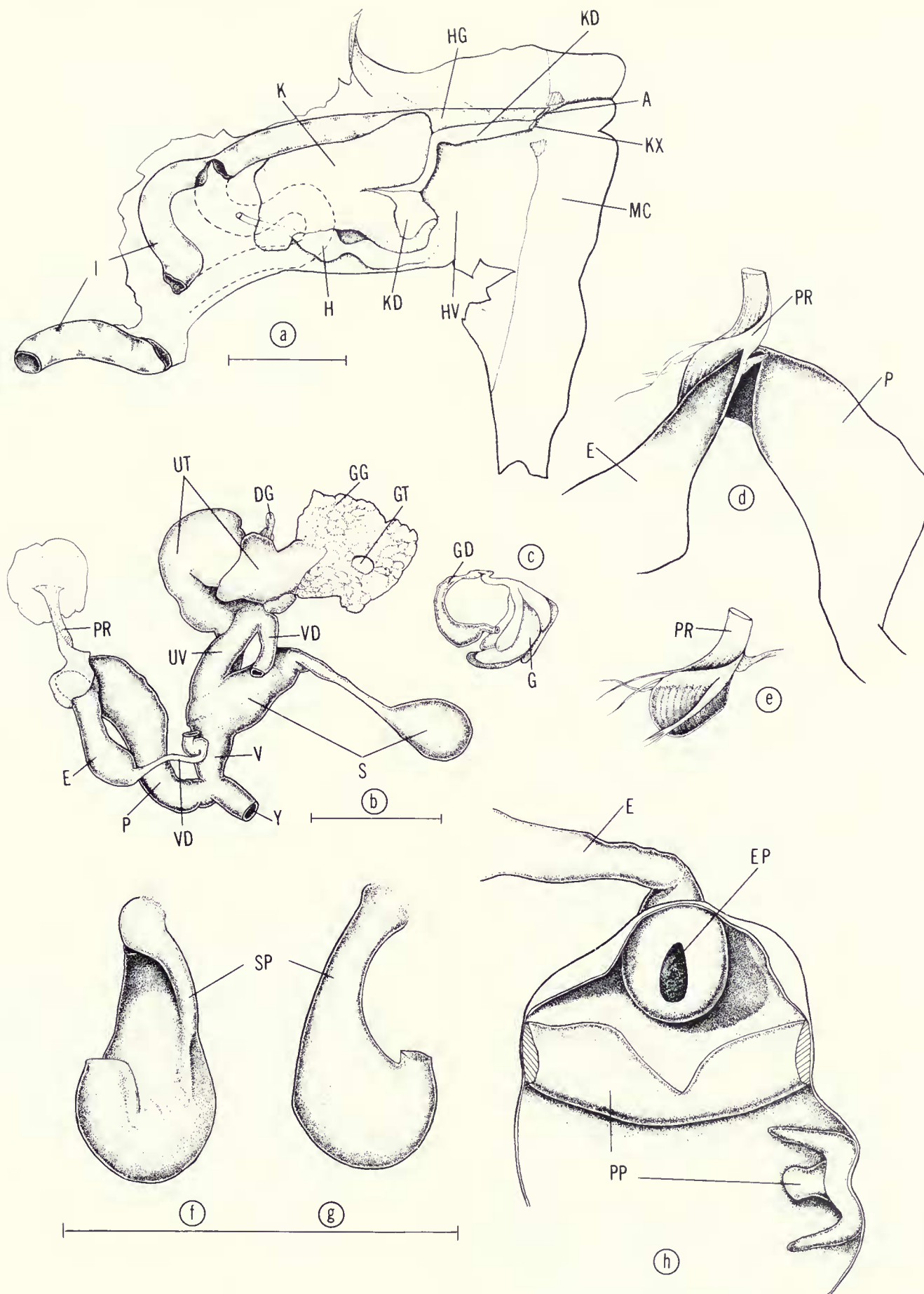


Fig. 75. Anatomy of the Fijian *Ba humbugi*, new species. Station VL-2, Tubarua, Viti Levu, Fiji. FMNH 153605: a, pallial region; b, genitalia; c, ovotestis and hermaphroditic duct; d-e, insertion details of penial retractor (PR) on epiphallus-penis junction; f-g, spermatophore; h, interior of apical penis region. Scale lines equal 1 mm. (SH).

Besides the keels, the alteration in ribbing pattern, very broad and regularly decoiling umbilicus, and flat spire represent departures from the *Sinployea* pattern.

Thus, generic recognition for *Maafu* is based on several shifts that combine to produce a drastically altered appearance. Local differentiation from a *Sinployea*-type stock is almost certain, but the structural gap is real and large.

I have chosen to honor the great Tongan leader Ma'afu, who unified the Lau Group in the 1850–1860s, by naming this genus after him. The specific name *thausasius* refers to the most unusual and wonderful shape of the shell.

***Maafu thausasius*, new species. Figure 76a–c.**

**Diagnosis.**—Shell relatively large, diameter 3.19–3.98 mm. (mean 3.49 mm.), with  $3\frac{1}{2}$ – $4\frac{1}{4}$  normally coiled whorls. Apex and spire depressed below level of subsutural keel, body whorl not descending or rarely very slightly deflected, H/D ratio 0.343–0.381 (mean 0.365). Apical sculpture of 10–15 (mean 12.2) narrow but prominent spiral cords. Postnuclear sculpture of high, broadly rounded, rather widely spaced radial ribs, 36–55 (mean 44.1) on the body whorl, whose interstices are about 2–5 times their width, and which become higher and more sharply defined on crossing keels. Ribs/mm. 3.59–4.74 (mean 4.08). Microsculpture of extremely fine radial riblets, barely visible at 96 $\times$  magnification and too obscured by the secondary spiral cording to be counted accurately, equally fine spiral riblets, and much more prominent secondary spiral cording, whose interstices are 1–3 times their width. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.82–3.15 times (mean 2.99) in the diameter, columellar-basal margin obtusely shouldered. Sutures deep, whorls strongly rounded above, after nucleus with a gradually increasing subsutural keel followed by a deep supra-peripheral sulcus, periphery a sharply protruded cordlike keel, a broader and shallower subperipheral sulcus, basal margin rounded to an obtusely shouldered columellar-basal angle, walls of umbilicus evenly rounded.

Although the form of *Maafu thausasius* recalls that of the Navutu-i-Loma endodontid *Zyzyxdonta alata* Solem (1976b, p. 466, fig. 198a–c), the larger size, beaded and numerous apertural barriers, "winglike" rib extensions, flat spire, and radial apical sculpture of the latter at once separate the two species. No Polyneesian Charopidae have an even slightly similar shape, and *M. thausasius* cannot be confused with any other species.

**Description.**—Shell relatively large, with slightly less than 4% moderately tightly coiled whorls. Apex and early spire depressed below plane of subsutural keel on succeeding whorls, last whorl not descending, H/D ratio 0.378. Sutures shallow, slightly denticulated by radial ribbing. Postapical whorls with a high subsutural ridge, becoming slightly less prominent near end of body whorl. Periphery of body whorl greatly protruded into a ridgelike keel, denticulated by crossing of major ribs, with a very prominent sulcus above and a less prominent one below periphery. Embryonic whorls  $1\frac{1}{4}$ , sculpture of about 12 very fine, closely spaced spiral ribs (partially eroded). Post-nuclear whorls with widely spaced, low, rounded, protractively sinuated radial ribs, 50 on the body whorl, that denticulate the periphery and whose interstices are 3–6 times their width. Microsculpture on early whorls of very fine radial riblets, crossed by slightly stronger secondary spiral cords. Microspiral riblets occasionally visible. On later whorls the radials become obsolete and the spirals slightly more prominent. Umbilicus broadly open, cup-

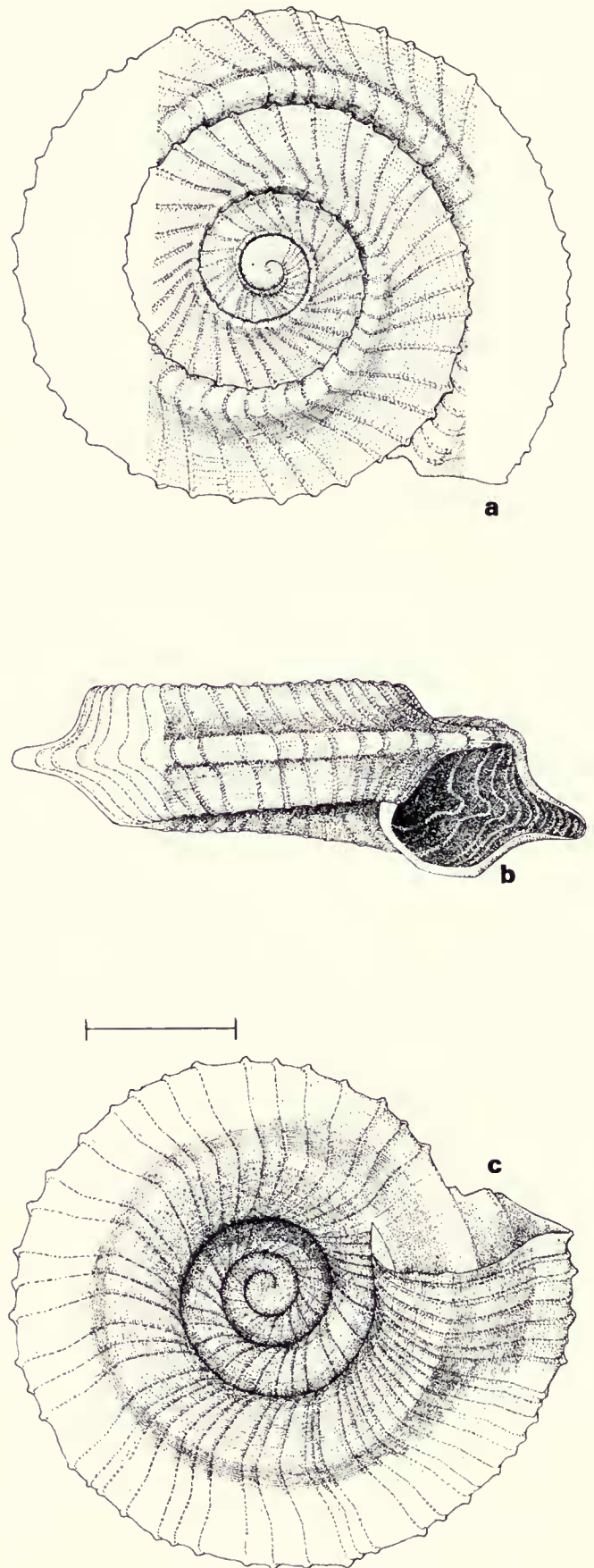


FIG. 76. a–c, *Maafu thausasius*, new species. Station 43, Nayau, Lau, Fiji. Holotype. BPBM 167233. (MM).



shaped, regularly decoiling, contained 2.98 times in the diameter. Color mainly leached from shell. Aperture subquadrangular with concave outer margins and rostrate periphery, inclined about 20° from the shell axis. Height of holotype 1.48 mm., diameter 3.92 mm.

*Holotype*.—Fiji: Lau Group, Nayau, Station 43, hillside ½ mile inland of Nauko at 250 ft. elevation. Collected at base of limestone cliff by H. S. Ladd on August 13, 1934. BPBM 167233.

*Range*.—Nayau, Lau Group, Fiji.

*Paratypes*.—Nayau, hillside ½ mile inland of Nauko (Station 43) at 250 ft. elevation (64 specimens, BPBM 167233).

*Remarks*.—The very striking subsutural ridge and peripheral keel immediately separate *Maafu thaumasius* from all other species of Polynesian Charopidae. It is most apt to be confused with *Zyzyx-donta alata*, a species of Endodontidae from Navutu-i-Loma that differs in having radial apical sculpture and apertural barriers of strong lamellae that are regularly beaded above. In addition the major ribs of *Z. alata* are prolonged into cup-shaped winglike structures when crossing the periphery (Solem, 1976b, p. 466, fig. 198a–c). The ribs in *M. thaumasius* only slightly denticulate the keel (fig. 76b).

Only 20% of the specimens were adult. Much of the material was fresh, but no specimens were collected alive.

#### Genus *Lauopa*, new genus

Shell extremely large, with about 4¼ normally coiled whorls. Apex and spire flat or slightly depressed, body whorl descending rapidly. Apical sculpture of about 22 very prominent spiral cords. Postnuclear whorls with high, widely spaced, strongly protractively sinuated radial ribs. Microsculpture of fine radials and finer spirals, no secondary cording. Umbilicus widely open, cup-shaped, regularly decoiling. Whorls flattened laterally above and slightly compressed laterally below rounded periphery. Parietal wall with median, high barrier, extending about ¼ whorl, with abrupt anterior descension, not expanded above. No palatal or columellar barriers. Anatomy unknown.

*Type species*.—*Lauopa mbalavuana*, new species.

Placement of this species in a distinct genus without any knowledge of its anatomy is based upon elimination of alternative classifications. Key features are the very large and numerous apical cords, presence of a single parietal barrier, absence of secondary spiral cording, very large size, and widely spaced radial ribbing. Species of *Graeffedon* from Samoa and Tonga are much smaller, have many more and shorter barriers, more crowded radial ribbing, and much narrower umbilici. They agree in lack of secondary spiral cording and the flat or nearly flat apex and spire. *Tuimalila* from Tonga also lacks secondary spiral cording, but differs in its narrow umbilicus, distinctly elevated spire, prominent and much more crowded radial sculpture, greatly reduced apical sculpture, total absence of apertural barriers, and smaller size. *Sinployea complementaria* (Mousson) from Upolu, Western Samoa, is only 4.92 mm. in mean diameter and lacks any apertural barriers (fig. 56b).

Possibly *Lauopa* may be related to the Micronesian genus *Semperdon*, but until live material can be obtained and dissected, no affinities can be determined. Generic recognition is given because there are major differences from any other genus known in this region. The name *Lauopa* refers to its occurrence in the Lau Archipelago. For convenience it is associated with the generalized Charopinae.

#### *Lauopa mbalavuana*, new species. Figure 77a–c.

*Diagnosis*.—Shell extremely large, diameter 6.67–8.37 mm. (mean 7.52 mm.), with 4¼–4¾ normally coiled whorls. Apex and spire flat, lower spire descending slightly, body whorl much more rapidly, spire protrusion less than ¼ body whorl width, H/D ratio 0.422–0.437 (mean 0.430). Apical sculpture of about 22 prominent spiral cords whose interstices are about equal to their width. Post-nuclear sculpture of high, prominent, protractively sinuated radial ribs, 39 on the body whorl in subadult, whose interstices are about 5–8 times their width, becoming extremely crowded and irregular on last third of body whorl in adult (fig. 77a). Ribs/mm. in juvenile 1.86. Microsculpture of extremely fine and crowded spiral and radial riblets, more than 20 radials between each pair of major ribs, spirals distinctly finer. No secondary spiral cording. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.72–2.76 times (mean 2.74) in the diameter, margins rounded. Whorls strongly rounded above and on periphery, slightly compressed laterally on upper and lower palatal margins. Parietal wall with single median, high barrier, extending posteriorly less than ¼ whorl, slightly expanded above, with abrupt descension at anterior end. No columellar or palatal barriers.

*Tuimalila pilsbryi* and *T. infundibulus* from Tonga (fig. 78a–f) both approach the size of *Lauopa mbalavuana* but lack the parietal barrier, have an elevated spire, much finer apical cording, and more crowded radial ribbing. All other Fijian and Polynesian species are much smaller in size.

*Description*.—Shell extremely large, with 4¾ moderately tightly coiled whorls. Apex and early spire slightly depressed below penultimate, last whorl descending rapidly, H/D ratio 0.437. Embryonic whorls 1½, sculpture eroded. Remaining whorls with remnants of protractively sinuate, low, rounded, widely spaced radial ribs whose interstices are 3–7 times their width, becoming extremely crowded on last third of body whorl. Microsculpture of very fine, close-set riblets crossed by even more crowded, low spiral ribs. Sutures deeply impressed, whorls strongly rounded above, flattened laterally above periphery. Color leached from shell with few vague flammulations remaining. Aperture circular, flattened laterally above periphery, inclined 25° from the shell axis. Parietal wall with one high, ridgelike barrier extending a little more than ⅓ of a whorl. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.72 times in the diameter. Height of holotype 3.66 mm., diameter 8.37 mm.

*Holotype*.—Fiji: Lau Group, Vanua Mbalavu, Station 78, a limestone hill between Valika and Mosomo Bay, ¾ mile inland at 200–250 ft. elevation. Collected under stones and logs in a dense forest by Yoshio Kondo and Elwood Zimmerman on August 9, 1938. BPBM 179554.

*Paratype*.—Lau Group: Vanua Mbalavu, a limestone hill between Valika and Mosomo Bay, ¾ mile inland (Station 78) at 200–250 ft. elevation, under stones and logs (1 specimen, BPBM 179554).

*Remarks*.—The adult holotype of *Lauopa mbalavuana* is a rather badly worn specimen, whereas the

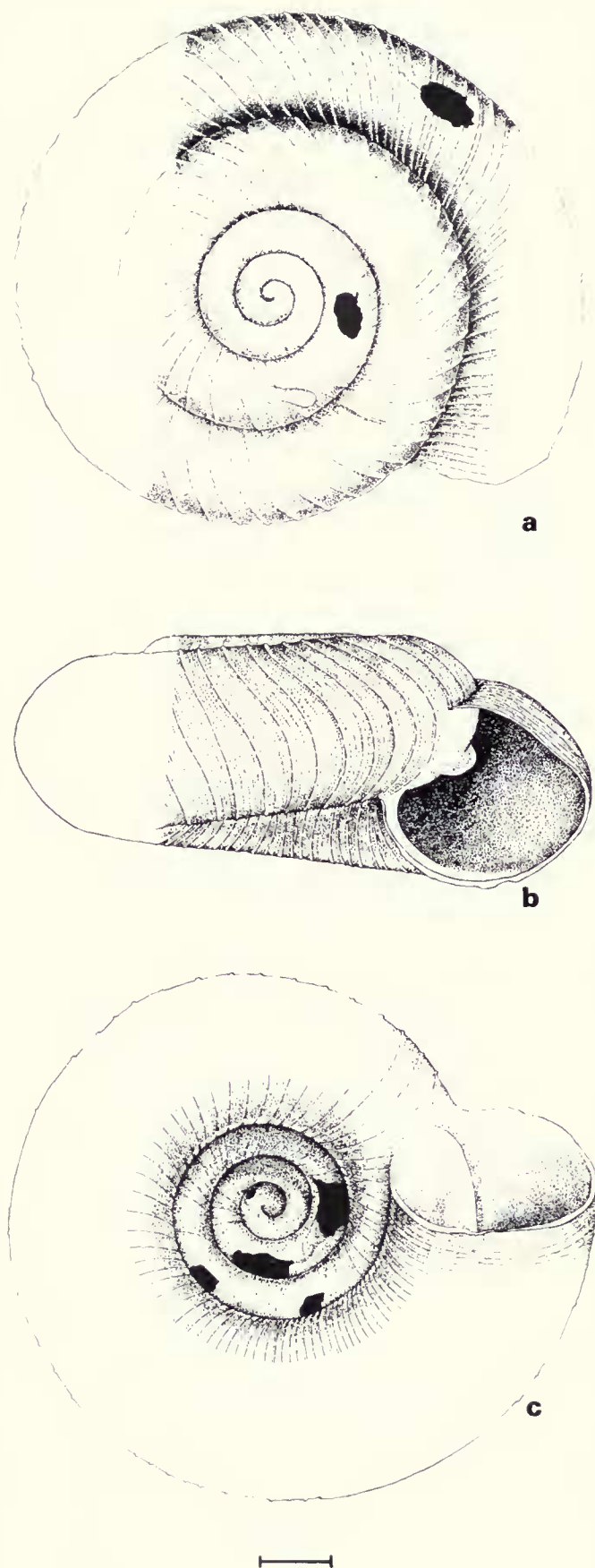


FIG. 77. a-c, *Lauopa mbalavuana*, new species. Station 78, Vanua Mbalavu, Lau, Fiji. Holotype. BPBM 179554. Scale line equals 1 mm. (MM).

juvenile subadult retains most of the apical and microsculpture. It is uncertain whether this is a living or extinct species because the better-preserved paratype apparently was leached out from coralline rock, fragments of which are cemented to the shell.

The only species of similar size, shape, and apical sculpture are the Tongan *Tuimalila infundibulus* and *T. pilsbryi*, neither of which have any apertural barriers.

#### Genus *Tuimalila*, new genus

Shell very large, with normally to loosely coiling whorls. Apex and spire moderately elevated. Apex with fine and crowded spiral cords, at least in one species with a secondary intrusion of radial swellings that appear under optical examination as primary radial ribs. Postnuclear sculpture of prominent, large, major radials and typical microsculpture. Umbilicus narrow, V-shaped, regularly de-coiling. Aperture relatively large. Pallial region as in *Sinployea*, a narrow strip of lung roof visible between arms of ureter, kidney lobes almost equal in size. Genitalia agreeing with *Sinployea* except for nearly apical pore in the vergie papilla and presence of a well-developed retractor muscle attached to the free oviduct head.

*Type species.*—*Tuimalila pilsbryi*, new species.

Although the Upolu *Sinployea complementaria* (Mousson) approaches the size of *Tuimalila* and several Rarotongan species had individuals within its size range, the two species grouped here average significantly larger, show a different pattern of whorl increment, and have distinctive patterns of apertural opening. Their apical sculpture has the spiral cords reduced in prominence and increased in number over that found in *Sinployea*, whereas at least in *T. pilsbryi* there is developed a secondary intrusion of radial swellings (fig. 2c, p. 11). These appear as radial ribs under optical microscopic inspection at 96 $\times$  and visually mimic the characteristic Endodontidae apical sculpture. Whether this same feature occurs in *T. infundibulus* cannot be determined until specimens with unworn apical sculpture are obtained for study.

Anatomical features show no characters incompatible with derivation from *Sinployea*, whereas the conchological changes are matters of degree rather than major shifts. Nevertheless, the change in apical sculpture and increase in size are major departures from the typical *Sinployea* pattern. The average mean diameter of the two species in *Tuimalila*, 6.16 mm., represents a 54% jump over the median mean diameter of *Sinployea* species and a 25% jump over the mean diameter, 4.92 mm., of *S. complementaria* (Mousson), the largest species in that genus. This size increase occurred with a slight actual decrease in whorl count and a marked increase in relative whorl widths. In *Sinployea* the median mean whorl count is  $4\frac{1}{8}$ —, whereas *Tuimalila infundibulus* has  $3\frac{3}{4}$ + and *T. pilsbryi* 4+ whorls. The result of this size increase combined with no increase in whorl count is to alter the growth pattern. The much more rapidly increasing whorl cross-section combines with the higher pallial surface to broaden the kidney (fig. 79a) and to fore-shorten the pallial organization.



Just as *Ba* represents a new experiment in altered growth pattern by increased spire height, so *Tuimalila* is a new pattern based on great increase in whorl width. As such, both merit generic separation from *Sinployea*.

The name *Tuimalila* commemorates the deceased famous tortoise, Tu'i Malila, which was resident in Tonga for many years and supposedly dated from the visit of Captain Cook (see Robb & Turbott, 1971).

***Tuimalila pilsbryi***, new species, Figures 78a–c, 79a–e.

*Charopa radicalis* Boettger, 1916 (not Mousson, 1871), Abhl. Senckenb. Naturf. Gesell., 36 (3), p. 290—Eua, Tonga.

**Diagnosis.**—Shell extremely large, diameter 5.88–6.99 mm. (mean 6.64 mm.), with 3¼–4¾ almost normally coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending slightly more rapidly, spire protrusion about ⅓–¼ body whorl width, H/D ratio 0.495–0.606 (mean 0.556). Apical sculpture of numerous extremely fine and regular spiral cords (fig. 2c, p. 11), with a gradual intrusion of low, rounded radial swellings that appear as fine, major radial ribs on last portion. Postnuclear sculpture of relatively narrow, prominent, V-shaped, strongly protractively sinuated radial ribs, 74–103 (mean 91.2) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 3.55–4.97 (mean 4.37). Microsculpture of very fine radial riblets, 5–12 between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets (fig. 2c–d). Umbilicus narrow, V-shaped, regularly decoiling, contained 4.48–6.50 times (mean 5.62) in the diameter, margins rounded. Whorl contours and aperture typical.

*Tuimalila pilsbryi* from Eua (fig. 78a–c) is a more depressed, larger shell with less descension of the body whorl, and has lower, less sharply defined radial ribs than does *T. infundibulus* (fig. 78d–f) from Vavau.

**Description.**—Shell extremely large, with 4 somewhat loosely coiled whorls. Apex and early spire moderately and evenly elevated, body whorl not descending more rapidly, H/D ratio 0.529. Embryonic whorls 1¾, first whorl with sculpture of about 33 very fine spiral riblets, last ¾ whorl showing a gradual emergence of low, broadly rounded, radial swellings, foreshadowing spire sculpture. Radial ribs on early spire low, broadly rounded, becoming more prominent and higher below. Radial ribs on body whorl protractively sinuated, prominent, 94 in number, whose interstices are 2–3 times their width. Microsculpture of very fine, closely set radial riblets with equally spaced, smaller spiral ribs. Sutures moderately impressed, whorls evenly rounded above, body whorl somewhat flattened laterally above periphery and slightly flattened on basal margin. Umbilicus open, V-shaped, last whorl decoiling slightly more rapidly, contained 4.86 times in the diameter. Color light yellow-white with numerous sinuated irregular reddish brown flammulations. Aperture ovate with somewhat flattened basal margin, inclined about 20° from shell axis. Height of holotype 3.53 mm., diameter 6.67 mm.

**Holotype.**—Tonga: Eua, Johanssen Plantation, 2 miles inland at 385 ft. elevation. Collected by H. S. Ladd on May 14, 1928. BPBM 87750.

**Range.**—Eua Island, Tonga.

**Paratypes.**—Eua (1 specimen, SMF 165341 collected by E. Wolf on June 5, 1909): Johanssen Plantation, 2 miles inland at 385–500 ft. elevation (5 specimens, BPBM 87750, BPBM 87719, BPBM 108565); main range on east side (Station T-22) of island at 1,000 ft. elevation in heavy forest (35 specimens, FMNH 152378).

**Remarks.**—Although there are a few striking quantitative differences (table XXXIX) between *Tuimalila pilsbryi* and *T. infundibulus*, the ribbing character and different aperture appearances immediately separate individuals of the two species. Although the intrusion of secondary radial ribbing into the apex was not seen in any specimens of *T. infundibulus*, all specimens of the latter were so worn that this may be present on that species also.

Living examples were common in fallen tree fern fronds.

Great pleasure is taken in dedicating this species to the late Henry A. Pilsbry, dean of terrestrial malacologists and mentor.

**Description of soft parts.**—Foot and tail equal to shell diameter in length, slightly tapering posteriorly, truncated anteriorly. Sole undivided longitudinally, transversely corrugated in preservative. Pedal grooves typical, suprapedal distinctly weaker than pedal, both uniting above tail, no caudal horn or middorsal groove developed. Slime network weak, without peculiarities. Head projecting in front of foot, ommatophores typical, eyespots large. Gonopore a broad slit, opening behind right rhinophore and below right ommatophore.

Body color yellow-white, a faint trace of grayish color on neck, ommatophores distinctly grayish.

Mantle collar (MC) thick, without obvious lobing, a broad black zone of color granules along inner margin, no glandular extension into pallial roof. Anus opening just inside pneumostome, slightly in front of external ureteric pore (KX).

Pallial region (fig. 79a) extending slightly more than ¾ whorl apically. Lung roof clear, no granulations. Kidney (K) about 3.0 mm. long, bilobed, with rectal arm slightly longer, reaching across hindgut onto parietal wall, very high at end of cavity, dished on posterior margin. Distance from anterior end to anus 2.1 mm. Ureter (KD) typical, a narrow strip of lung roof visible between arms that open at a slight angle. Heart (H) more than ½ length of kidney, slightly angled to hindgut. Principal pulmonary vein (HV) unbranched, relatively conspicuous. Hindgut (HG) without unusual features.

Ovotestis a single clump of palmately clavate alveoli, lying parallel to whorl sides and occupying almost ½ whorl above stomach apex. Hermaphroditic duct iridescent, slightly kinked in middle areas, narrowing abruptly at point where it starts along albumen gland, reflexing up to enter junction of talon and carrefour (fig. 79e). Albumen gland with rather large acini, surface deeply indented by other organs, general shape squarish. Talon (fig. 79e, GT) globular, without a distinct shaft, joining hermaphroditic duct directly at head of carrefour (X). Latter ¾ diameter of talon, tapering into head of prostate-uterus. Prostate (DG) with many very prominent and long alveoli complexly folded against wall of uterus, opening into groove on inner wall of uterine chambers. Prostate-uterus folded back on itself for part of length. Uterus (UT) typically bipartite, lower chamber with thick, glandular walls.

Vas deferens (VD) wide in diameter with rather thick, pilastered, glandular walls until just before penioviducal angle, becoming very slender, reflexing upward. Epiphallus (E) about ¾ length of penis, inserting into penis to one side of penial retractor, receiving vas deferens laterally on very swollen head, lower ¾ more slender. Internally with Y valve and plug apically, lower portion with longitudinal pilasters running into epiphallic pore (fig. 79c). Penial retractor (PR) very short, arising on diaphragm, inserting directly onto head of penis. Penis (P) about 2.4–2.5 mm. long, club-shaped, swollen medially, tapering slightly to atrial junction. Internally with typical pocket stimulator producing medial hulse, apically (fig. 79c–d) with vergic papilla and circular muscle band on wall below it. Atrium (Y) about ⅓ length of penis, tapering gradually.



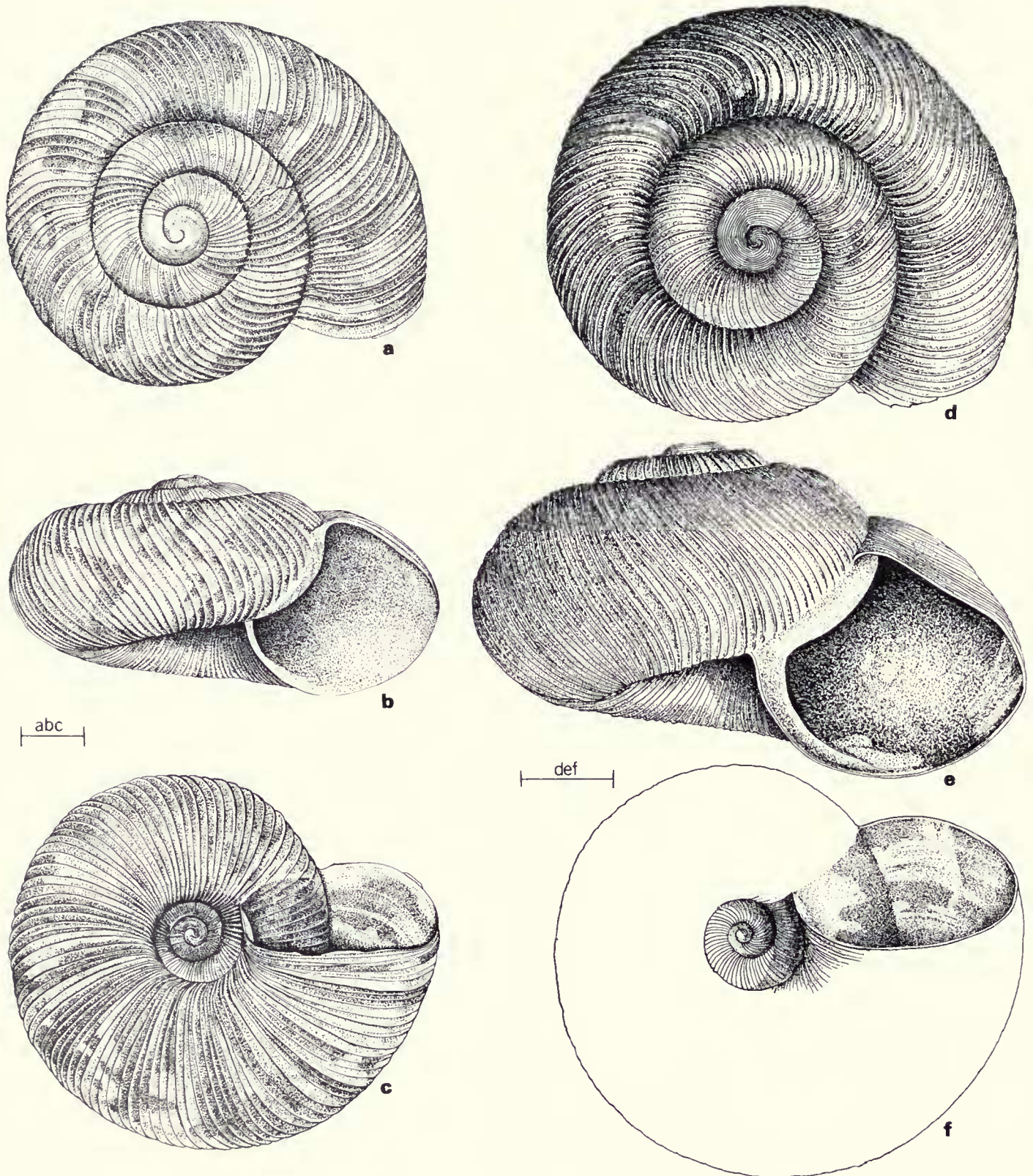


FIG. 78. a-c, *Tuimalila pilsbryi*, new species. Johanssen Plantation, Eua, Tonga. Holotype. BPBM 87750; d-f, *Tuimalila infundibulus* (Hombron & Jacquinot). Lectotype of *Patula radicalis* Mousson. Zoologisches Institut der Universität Zurich. Scale lines equal 1 mm. (a-c, SH; d-f, SG).



TABLE XXXIX. — RANGE OF VARIATION IN FIJIAN AND TONGAN ENDEMIC GENERA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER	H/D RATIO
<u>Ba</u> <u>humbugi</u>	4	I R R E G U L A R		2.17(1.84–2.50)	2.72(2.30–3.32)	0.801(0.752–0.842)
<u>Maafu</u> <u>chaumasius</u>	65	44.1(36–55)	4.08(3.59–4.74)	1.28(1.12–1.51)	3.49(3.19–3.98)	0.365(0.343–0.381)
<u>Lauopa</u> <u>mbalavuana</u>	2	39	1.86	3.24(2.81–3.66)	7.52(6.67–8.37)	0.430(0.422–0.437)
<u>Tuimalila</u> <u>infundibulum</u>	156	88.3(75–96)	4.88(4.17–5.37)	3.49(2.88–4.18)	5.68(4.97–6.86)	0.616(0.547–0.710)
<u>T. pilsbryi</u>	42	91.2(74–103)	4.37(3.55–4.97)	3.69(3.07–4.12)	6.64(5.88–6.99)	0.556(0.495–0.606)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	
	<u>humbu.</u>	3 3/8(3 1/8–3 1/2)	C L O S E D		12.0(11–13)	
	<u>thaum.</u>	4 1/8(4–4 3/8)	1.16(1.05–1.32)	2.99(2.82–3.15)	12.2(10–15)	
	<u>mbala.</u>	4 1/2(4 1/4–4 3/4)	2.75(2.42–3.07)	2.74(2.72–2.76)	22	
	<u>infun.</u>	3 3/4+(3 1/2–4 1/8)	1.04(0.86–1.32)	5.47(4.47–7.15)	MANY REDUCED	
	<u>pilsb.</u>	4+(3 3/4–4 3/8)	1.19(1.05–1.24)	5.62(4.48–6.50)	MANY REDUCED	
		SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW	PR	
	<u>humbu.</u>	0.37(0.25–0.46)	0.97(0.82–1.12)	0.379(0.300–0.483)	–	
	<u>thaum.</u>	DEPRESSED	0.75(0.66–0.84)	--	–	
	<u>mbala.</u>	0.15(0.07–0.23)	2.03(1.76–2.28)	0.069(0.037–0.100)	1	
	<u>infun.</u>	0.36(0.20–0.53)	1.94(1.74–2.07)	0.185(0.113–0.258)	–	
	<u>pilsb.</u>	0.47(0.33–0.66)	2.06(1.91–2.20)	0.223(0.159–0.308)	–	

Free oviduct (UV) surmounted by a retractor muscle, swollen above, tapering rapidly with muscular walls, then suddenly expanding to form a thin-walled sac gradually tapering to spermathecal junction. Spermatheca (S) with ovate head lying next to albumen gland, shaft slender to base of uterine fold, lower portion rapidly expanding to equal penis in width. Vagina (V) equal in diameter to median free oviduct, very short, without prominent internal features.

Free muscle system unusual only in having a very large muscle from the free oviduct apex attached to columellar retractor just above tentacular retractors. Right ommatophoral retractor passing through penioviducal angle. Tentacular retractors unite with tail fan just above junction of latter with buccal retractor.

Stomach occupying  $\frac{3}{4}$  whorl after reaching expanded size. Intestinal loops highly compacted, hindgut typical.

(Based on FMNH 152378, 4 adults 5.9–6.1 mm. in diameter.)

### **Tuimalila infundibulum** (Hombron & Jacquinot, 1841). Figure 78d–f.

*Helix infundibulum* Hombron & Jacquinot, 1841, Ann. Sci. Nat. Zool., (2) 16, p. 64—Vavao, Tonga Islands; Hombron & Jacquinot, 1852, Voy. Pol. Sud, Astrolabe et Zélée, Atlas, pl. 6, figs. 25–28—Vavao, Tonga; Rousseau, 1854, Voy. Pol. Sud, Astrolabe et Zélée, Atlas, 5, p. 20.

*Patula (Patula) radicalis* Mousson, 1871, J. de Conchyl., 19, pp. 12–13, pl. 3, fig. 3—Vavao, Tonga Islands.

*Helix radicalis* (Mousson), Pfeiffer, 1876, Monog. helic. viv., 7, p. 164.

*Helix crebriflammis* Pfeiffer, 1876, Monog. helic. viv., 7, p. 148—lists *infundibulum* Hombron & Jacquinot, 1841, as a questionable synonym of this New Zealand species.

*Charopa radicalis* (Mousson), Tryon, 1886, Man. Conchol., (2) 2, p. 210.

*Endodonta (Flammulina) radicalis* (Mousson), Hedley, 1893, Nautilus, 7 (3), p. 35.

*Endodonta (Charopa) radicalis* (Mousson), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35.

*Rhytida (Ouagapia) radicalis* (Mousson), Möllendorff, 1903, Syst. Conchyl. Cab., I, 12, b, p. 83, pl. 13, figs. 12–15.

**Diagnosis.**—Shell very large, diameter 4.97–6.86 mm. (mean 5.68 mm.), with  $3\frac{1}{2}$ – $4\frac{1}{8}$  rather loosely coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending much more rapidly, spire protrusion a little less than  $\frac{1}{8}$  body whorl width, H/D ratio 0.547–0.710 (mean 0.616). Apical whorls worn in all examples examined, occasionally fine traces of weak and crowded spiral cords visible under oblique lighting. Postnuclear sculpture of high, thin, sharply defined, strongly protractively sinuated radial ribs, 75–96 (mean 88.3) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 4.17–5.37 (mean 4.88). Microsculpture a lattice of very fine radial and spiral riblets, 4–10 microradials between each pair of major ribs. No secondary spiral cording. Umbilicus narrow, V-shaped, regularly decoiling, contained 4.47–7.15 times (mean 5.47) in the diameter, margins rounded. Whorl contours and aper-

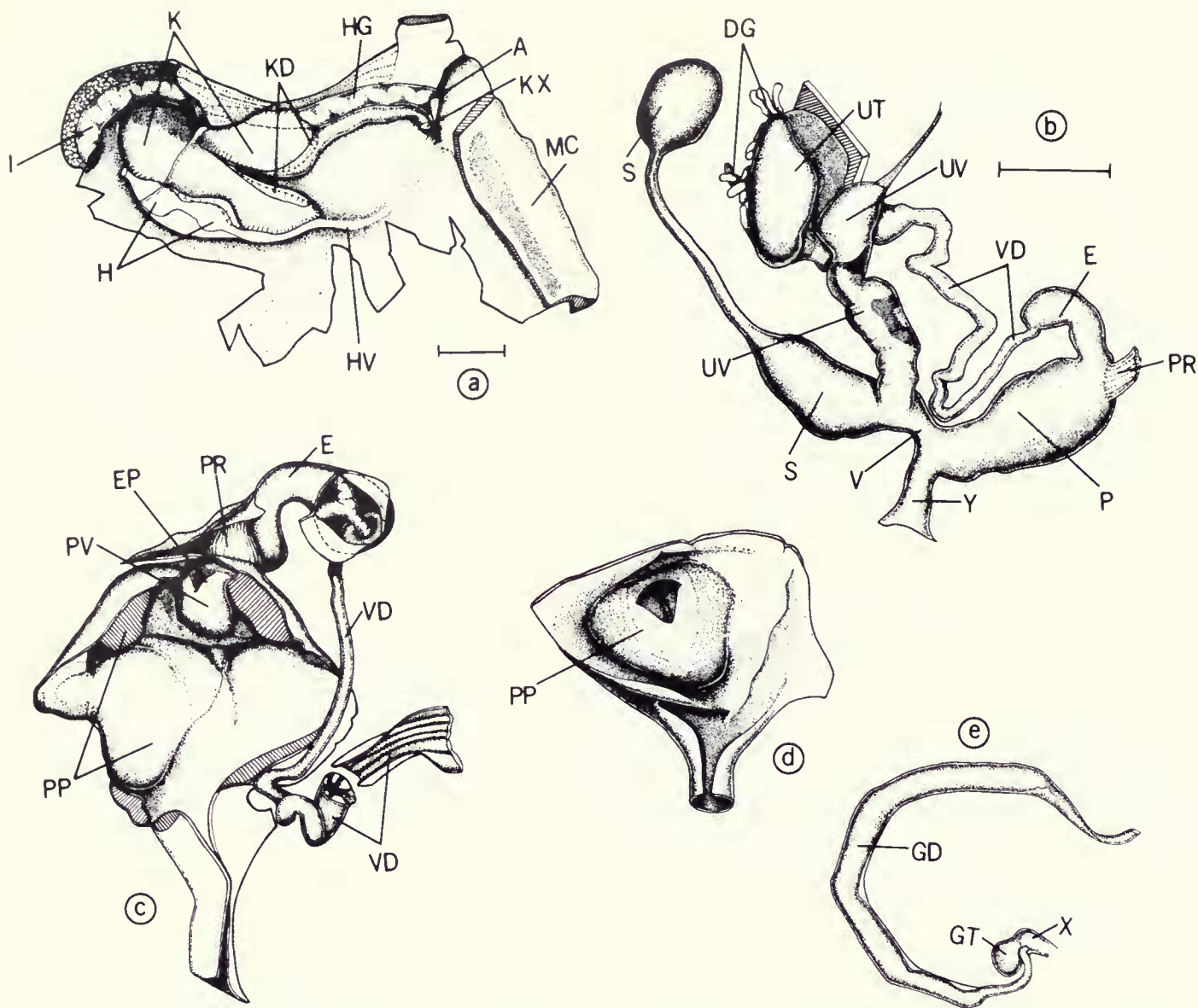


FIG. 79. Anatomy of the Tongan *Tuimalila pilsbryi*, new species. Station T-22, Eua, Tonga. FMNH 152378: a, pallial region; b, pallial and terminal genitalia; c, interior of penis, epiphallus and vas deferens; d, detail of major penial stimulator; e, talon and hermaphroditic duct. Scale lines equal 1 mm. (SH).

tural inclination normal. Color with narrow, wavy reddish flammulations, a tendency for broad circular supraperipheral and basal reddish zones evident in many individuals.

*Tuimalila infundibulus* (fig. 78d-f) is smaller, has a less protruded spire, but a greater H/D ratio than does *T. pilsbryi* (fig. 78a-c). The latter has less crowded ribbing, and the apical whorls show a clear radial element (fig. 2c, p. 11) that apparently is lacking in *T. infundibulus*. No other Polynesian Charopidae even approach the size of this species.

**Description of *radicalis*.**—Shell very large, with 4 rather loosely coiled whorls. Apex and spire moderately elevated, slightly rounded above, body whorl descending more sharply, H/D ratio 0.634. Apical whorls 1%, sculpture of extremely fine and crowded spiral ribs that are barely visible except under strong lateral lighting. Postnuclear whorls with irregular, high, rounded, strongly protractively sinuated radial ribs, about 92 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of very fine, crowded radial riblets, crossed by slightly finer and more crowded spiral riblets. Sutures

deep, whorls shouldered above, strongly flattened laterally above periphery, with evenly and gently rounded subperipheral margins. Color light yellowish brown with very irregular radial reddish maculations that coalesce to form a broad and a narrow band above the periphery, a wide subperipheral plus a faint umbilical color band. Umbilicus narrowly open, V-shaped, regularly decoiling, contained 5.55 times in the diameter. Aperture subcircular, strongly flattened laterally above periphery, inclined almost 25° from the shell axis. Height of lectotype 3.82 mm., diameter 6.02 mm.

**Lectotype of *radicalis*.**—Tonga: Vavau. Collected by Dr. E. Graeffe. Zoologisches Museum der Universität Zurich.

**Range.**—Vavau Island, Tonga.

**Paratypes.**—Zurich, FMNH 116982.

**Material.**—Vavau (20 specimens, RSM, AMS, FMNH 46222, SMF 165340, BPBM 54361, BPBM 167432); Talau Id., 1 mile west (Station T-7) of Neiafu at 400 ft. elevation in dense low forest (62 specimens,



FMNH 152423); Mo'ungalafa, near Tu'anuku (Station T-9), about 14 miles southwest of Neiafu at 700 ft. elevation in heavy forest (2 specimens, FMNH 152207); Muitoulo (Station T-10), about 15 miles west of Neiafu at 500 ft. elevation in heavy forest (19 specimens, FMNH 152290); Pangai Motu Id. (Station T-11), 3 miles south of Neiafu at 200 ft. elevation (4 specimens, FMNH 152357); Makave village (Station T-12), 2½ miles southeast of Neiafu at 200 ft. elevation (1 specimen, FMNH 152348); Longomapu (Station T-14), 16 miles southwest of Neiafu in heavy forest at 400 ft. elevation (14 specimens, FMNH 152380); Leimatu'a (Station T-17), 9 miles north of Neiafu at 500 ft. elevation (2 specimens, FMNH 152323). "Tongatapu" (error) (22 specimens, Zurich, FMNH 116983). Erroneous data (3 specimens, FMNH 46243, IRB).

**Remarks.**—The name *Helix infundibulum* generally has been overlooked in the literature since Pfeiffer (1876) tentatively suggested it might be a synonym of the New Zealand *Flammulina crebriflammis* (Pfeiffer). Comparison of the type illustrations of *infundibulum* and *radialis* leaves no doubt that they depict the same species. I could not locate type material of *Helix infundibulum*.

Möllendorff's reference of this species to *Ouagapia* supposedly was based on work by Semper showing this species to have paryphantid dentition. I suspect that this was caused by a misreading of Semper (1874, p. 136), who stated that *O. gradata* was a paryphantid and that probably many of the other "*Patula*" from the same area were also paryphantids.

Extensive collections on Tongatapu in 1966 by Laurie Price failed to reveal any specimens of this species, hence I consider the material in the Mousson collection to be mislabeled. Unfortunately, all of the material taken on Vavau was dead so that *Tuimalila infundibulus* could not be dissected. Collections were made during a severe drought, and no living material was obtained of *Sinployea vicaria paucicosta* from some of the same stations.

At Station T-7 one individual had the remains of an egg capsule with an embryonic shell dried inside. Despite the narrow umbilicus, evidently the eggs are deposited within the umbilical opening. Although this practice is common in the Endodontidae (Solem, 1976b, pp. 26–30), this is the only Polynesian Charopidae that showed evidence of this trait.

### Genus *Lagivala*, new genus

Generally minute Charopidae with 3%–4% tightly coiled whorls. Apex and spire depressed (*demani*), flat (*davidi*), to moderately elevated, body whorl descending much more rapidly. Apical sculpture of 10–14 fine spiral cords. Postnuclear sculpture of prominent to very fine (*minusculus*) radial ribs, microsculpture typical, no secondary spiral cording. Umbilicus very widely open, cup-shaped, narrow only in *minusculus*. Periphery usually strongly compressed laterally (except *microglyphis*), umbilical margin rounded (*microglyphis*, *minusculus*) to strongly shouldered (*macroglyphis*). Sutures channeled in *macroglyphis*, *microglyphis*, and *minusculus*. Shell unicolored without darker flammulations. Parietal wall with 2 or 3 large barriers

(only 1 in *minusculus*), extending posteriorly from  $\frac{3}{4}$  of a whorl to line of vision; where 2 parietals only, apparently a 3rd is sometimes displaced onto columellar margin by partial detachment of parietal wall. Palatal barriers 3 to 6, short, very deeply recessed crescents or elongated lamellar blades situated near posterior margin of parietals, in *minusculus* only a long single barrier lying partly on columellar and partly on basal margin. Anatomy unknown.

**Type species.**—*Lagivala vivus*, new species.

*Lagivala* and *Vatusila* present generally contrasting patterns of structure (fig. 80–85). *Lagivala* has the body whorl laterally compressed (except for *microglyphis* and some *demani*); *Vatusila* has the body whorl flattened above the periphery. *Lagivala* lacks secondary spiral cording; *Vatusila* (except *vaitupuensis*) has secondary spiral cording. *Lagivala* has deeply recessed, short, and crescentic palatal barriers (except *minusculus* and some *demani*); *Vatusila* has fewer, much longer, and less deeply recessed palatals. *Lagivala* has very long and rather complexly twisted, high parietals; *Vatusila* shows a strong tendency toward fusion and reduction of the parietals. *Lagivala* has a very wide, cup-shaped umbilicus (except *minusculus*); *Vatusila* a U-shaped, narrower umbilicus (cup-shaped only in *eniwetokensis*). *Lagivala* has a relatively low spire; *Vatusila*, a high spire (except *eniwetokensis*). They agree in major sculpture and rib spacing, but only because both taxa exhibit an unusually wide range of types. Several *Lagivala* show a tendency toward channeling of the sutures, but others show no evidence of this change. Despite overlapping distributions and lack of anatomical evidence, I have no hesitation in considering them to be phyletically separate experiments in apertural constriction.

From the above list of comparisons, it is evident that two species are atypical. *Vatusila eniwetokensis* has the flat spire and cup-shaped umbilicus of *Lagivala*. Its possession of prominent secondary spiral cording (fig. 86f), gradual descension of the upper parietal (fig. 85e), rounded body whorl with flattening restricted to above the periphery, shorter parietals, and relatively narrow umbilicus (table XL) are characters that I consider to be more significant than the probably linked spire and umbilical shape changes. *Lagivala minusculus* may be incorrectly placed here, but insufficient data are available to propose generic separation. Temporary classification within *Lagivala* is a conservative and reasonable treatment pending more information.

Similarities to other genera are few. *Graeffedon* (figs. 86, 88) is much, much larger with short simple parietals and narrower, much less deeply recessed palatals that have abrupt anterior descension, a narrower, V-shaped umbilicus, and prominent, darker color flammulations. Other Melanesian and Polynesian taxa lack any apertural barriers. Of the Micronesian genera, *Palikirus* (fig. 91d–f) has only a single parietal barrier, a much narrower, V-shaped umbilicus, and much more widely spaced ribbing. *Jokajodon* (fig 92a–f) has very fine ribbing, many complicated apertural barriers, and secondary spiral cording. *Pal-*

TABLE XL. — RANGE OF VARIATION IN LAGIVALA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.			
<u>davidi</u> (Ladd)	1	70 or 87	15.9 or 19.8			
<u>vivus</u>	2	62.5(62-63)	11.47(11.39-11.55)			
<u>minusculus</u>	1	121	24.9			
<u>macroglyphis</u> (Rensch)	82	62.5(51-74)	11.16(9.86-12.46)			
<u>microglyphis</u> (Rensch)	5	95.5(86-101)	17.9(14.8-20.8)			
<u>demani</u> (Tapperone- Canevari)	42	79.0(56-106)	13.09(9.85-19.4)			
NAME	HEIGHT	DIAMETER	H/D RATIO			
<u>davidi</u> (Ladd)	0.7	1.4	0.500			
<u>vivus</u>	0.84	1.75(1.72-1.77)	0.483(0.477-0.490)			
<u>minusculus</u>	0.63	1.55	0.404			
<u>macroglyphis</u> (Rensch)	0.95(0.89-1.02)	1.73(1.64-1.89)	0.553(0.539-0.580)			
<u>microglyphis</u> (Rensch)	0.71(0.66-0.74)	1.63(1.55-1.74)	0.434(0.425-0.457)			
<u>demani</u> (Tapperone- Canevari)	0.85(0.76-0.95)	1.90(1.73-2.07)	0.448(0.416-0.518)			
WHORLS	UMBILICUS	H/U RATIO	APICAL CORDS			
<u>davidi</u>	3 1/2	0.51	2.62	UNKNOWN		
<u>vivus</u>	4	0.68(0.67-0.69)	2.82(2.61-3.03)	UNKNOWN		
<u>minus.</u>	3 3/8	0.30	5.22	10		
<u>macro.</u>	4 3/8-(4 1/8-4 5/8)	0.85(0.79-0.94)	2.03(2.00-2.08)	11-12		
<u>micro.</u>	3 7/8(3 3/4-4)	0.65(0.59-0.72)	2.54(2.41-2.61)	Circa 11		
<u>demani</u>	4 1/8+(3 3/4-4 1/2)	0.72(0.58-0.82)	2.64(2.48-3.03)	12.1(10-14)		
	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW	PR	C	P
<u>davidi</u>	FLAT	0.51	-----	2	0 or 1	3 or 4
<u>vivus</u>	FLAT	0.59	-----	3	0	6
<u>minus.</u>	0.05	0.42	0.118	1	0	1
<u>macro.</u>	0.07(0.04-0.10)	0.54(0.53-0.59)	0.131(0.076-0.188)	2	1	5
<u>micro.</u>	0.05	0.54	0.091	2	1	3-5+0-1
<u>demani</u>	FLAT OR DEPRESSED	0.61(0.58-0.67)	FLAT OR DEPRESSED	2-3	0-1	0-3-4

line (figs. 94-96) has secondary spiral cording, looser whorl coiling, and less deeply recessed palatals.

Known species of *Lagivala* are from Eastern Indonesia and West Irian (*L. demani*); New Britain, Bismarck Archipelago (*L. microglyphis* and *L. macroglyphis*); Viti Levu, Fiji (*L. vivus* and *L. minusculus*); and Funafuti, Ellice Islands (*L. davidi*). Except for the New Britain collections in shore drift and some sets of *L. demani*, only one or two examples are known of each despite intensive collecting efforts. Additional species will quite probably be discovered in intermediate areas since few attempts have been made at sampling the minute litter fauna.

The similarities of all *Lagivala* except *L. minusculus* are covered in the species accounts. Apparently, partial detachment of the parietal wall has resulted in the 3rd parietal becoming a columellar barrier in the Bismarck species and some populations of *L. demani*. Partial palatal barrier reduction in some examples of

*L. microglyphis* shows how the reduced number in *L. davidi* could be derived. The channeled suture of *L. minusculus* agrees with the Bismarck species, whereas its peculiar columellar-palatal barrier could be derived from the 3rd parietal or columellar by downward, rather than upward, twisting of the anterior portion.

In previous publications (Solem, 1958b, 1959a) I have used the genus *Beilania* Preston (1913, p. 433) for *L. demani* and several other species. Despite intensive search over 13 years, I have not been able to locate any specimens of *Beilania demani* Preston, 1913, in museum or private collections. Although the missing types may yet appear, the probabilities are that they will not be located in the immediate future. Preston's description places the parietals as being subperipheral, and the palatal wall is without barriers. In the absence of any specimens, I am reluctant to use the name *Beilania* for this group until the structures of the type species are known in regard to spire elevation, form and length of the parietals, actual rib count, and actual absence of the palatal barriers. Possibly *Lagivala* and *Beilania* are synonymous, but it is equally possible that *Beilania inopina* is more closely related to the Philippine-Indonesian species, *Beilania philippinensis* (Semper, 1874) (see Solem, 1957, pp. 7-8, fig. 3). That species has a narrower, V-shaped umbilicus, looser whorl coiling, a single crescentic parietal with gradual anterior descension, and three nodular palatals that are near the lip margin and often on a heavy callus much as in *Palline notera* and *P. biakensis*. The two latter species (figs. 94-96) differ in having prominent secondary spiral cording, tighter coiling, a much thicker body whorl, narrower umbilicus, and very differently shaped apertural barriers. *Beilania philippinensis*, although not dissected, shows major conchological differences from *Lagivala demani* and the more eastern species of *Lagivala*. Rather than propose an additional generic name for the Philippine-Indonesian species, I prefer to use *Beilania* for that species and the genotype, pending availability of additional material and soft parts for dissection.

*Lagivala* is the Fijian nickname, meaning "the long fellow," applied to the famous chief Qaraniqio or Dakuwaqa of the Rewa District in Viti Levu, Fiji.

#### *Lagivala davidi* (Ladd, 1968).

*Ptychodon* species A, Ladd, 1958, J. Paleont., 32 (1), p. 189, pl. 30, figs. 13-15—166-170 ft. in deep boring at Funafuti, Ellice Islands (Pleistocene or Recent).

*Ptychodon davidi* Ladd, 1968, J. Paleont., 42 (3), p. 857, fig. 1—170 ft. in deep boring, Funafuti, Ellice Islands.

**Diagnosis.**—A very small species with less than 3½ tightly coiled whorls. Apex and spire flat, body whorl descending slightly, H/D ratio about 0.500. Apical whorls 1½, sculpture of fine spiral cords. Postnuclear whorls with prominent, rounded, almost vertically sinuated radial ribs, about 70-87 on the body whorl. Micro-sculpture of fine radial and finer spiral riblets. Umbilicus widely open, cup-shaped, regularly decoiling, contained about 2.60 times in the diameter, margins weakly shouldered. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally, with evenly rounded outer margin. Parietal barriers 2, agreeing in



structure with the upper pair in *L. vivus*. Outer wall with 3 deeply recessed palatals, short and crescentic, a 4th barrier located at baso-columellar margin of adults that may be either a columellar or a palatal barrier.

*Lagivala vivus* (fig. 80a–c) differs from *L. davidi* in having three parietals, six palatals, and fewer major radial ribs. *Lagivala minusculus* (fig. 80d–f) has only a single parietal and one peculiar palatal. *Lagivala macroglyphis* and *L. microglyphis* (fig. 81a–f) have elevated spires and more palatal barriers.

**Holotype.**—Deep boring from Funafuti, Ellice Islands, at 170 ft. depth. AMS F.52343.

**Range.**—Fossil at Funafuti, Ellice Islands.

**Material.**—Only the holotype and lost specimen initially studied by Ladd (1958) are known.

**Remarks.**—The juvenile holotype has three deeply recessed palatals in the aperture, whereas the lost example had an additional barrier at or near the baso-columellar margin. I am uncertain whether this was a columellar or palatal barrier. Differences from *L. vivus* are covered in the diagnosis.

#### ***Lagivala vivus*, new species. Figure 80a–c.**

**Diagnosis.**—Shell very small, diameter 1.72–1.77 mm. (mean 1.75 mm.), with about 4 tightly coiled whorls. Apex and spire flat or very slightly depressed below level of penultimate whorl, body whorl descending moderately, H/D ratio 0.477–0.490 (mean 0.483). Apical sculpture of fine and crowded spiral cords, worn off over most of surface. Postnuclear whorls with high, rounded, sharply defined, almost vertically sinuated, rather crowded radial ribs, 62–63 (mean 62.5) on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 11.39–11.55 (mean 11.47). Microsculpture of fine radial riblets, 5–8 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. No secondary spiral cording present. Umbilicus widely open, cup-shaped, regularly decoiling, contained 2.61–3.03 times (mean 2.82) in the diameter, margins slightly shouldered, walls of umbilicus moderately flattened internally. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally with evenly rounded outer margin. Parietal barriers 3, extending posteriorly more than  $\frac{1}{4}$  whorl: upper a high, thin, bladeliike lamella, slightly elevated and expanded above on posterior eighth, with abrupt descension at anterior end after even elevation from posterior portion; 2nd slightly higher and more broadly expanded on posterior quarter, equal in height to 1st during middle section, with sinuated descension over anterior 8th; 3rd located just above parietal-columellar margin, much lower than 2nd, weakly elevated and expanded above on posterior half, with gradual descension to point just inside lip edge. Columellar wall without barriers. Palatal barriers 6, deeply recessed, short and crescentic: lower at baso-columellar margin, relatively low, visible only by tilting of aperture; 2nd twice height of 1st, longer, slightly flattened on top, with relatively sharp anterior descension; 3rd and 4th slightly shorter and  $\frac{2}{3}$  height of 2nd with more gradual anterior descension; 5th supraparaparietal, equal in height to 2nd, with more gradual anterior descension; 6th midway to palatal-parietal margin, a deeply recessed, low, and lamellate tubercle.

*Lagivala vivus* is readily identified by possessing a third parietal and six palatals. *Lagivala davidi* has more ribs, only two parietals, and three palatals, but obviously is closely related. The Bismarck *L. macroglyphis* and *L. microglyphis* (fig. 81a–f) have much more elevated spires, two parietals, a prominent columellar barrier, and only five palatals. *Lagivala demani* from Indonesia and West Irian has only three or

four palatals, a depressed spire, and usually only two parietals.

**Description.**—Shell very small, with 4 tightly coiled whorls. Apex and spire slightly depressed, body whorl descending moderately, H/D ratio 0.477. Embryonic whorls almost  $1\frac{3}{4}$ , traces of fine spiral cording present, surface mostly eroded. Postnuclear whorls with high, prominent, sharply defined, crowded radial ribs, 63 on the body whorl, whose interstices are 2–4 times their width. Microsculpture of fine radial riblets, 5–8 between each pair of major ribs, crossed by barely visible and extremely crowded spiral riblets. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally, with evenly rounded outer margin. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.61 times in the diameter, margins shouldered, inside walls flattened. Color uniform light reddish yellow, without distinct flammulations. Aperture ovate, compressed laterally, with evenly rounded outer margin, inclined about 5° from shell axis. Apertural barriers as in diagnosis above. Height of holotype 0.86 mm., diameter 1.76 mm.

**Holotype.**—Fiji: Viti Levu, Station 54, hillside at Telenaua, 48.3 miles west of Suva by Belt Road at 60 ft. elevation, back of Serua village. Collected in leaf mould by Yoshio Kondo, Elwood Zimmerman, and C. M. Cooke, Jr., on July 26, 1938. BPBM 178598.

**Range.**—South coast of Viti Levu, Fiji.

**Paratype.**—Viti Levu: Lami Ridge, west of Suva (Station 47) on limestone rock (1 specimen, BPBM 178488); Nandarivatu (Station F-16), ridge slope at 2,500 ft. elevation (1 specimen, FMNH 168364).

**Remarks.**—Only three dead specimens are known. They agree in apertural features, which clearly distinguish them from other *Lagivala*. Attempts in 1962 to collect additional specimens were unsuccessful, and in 1965 L. Price obtained one dead adult.

The name *vivus* is to contrast this species with its nearest relative, *Lagivala davidi* (Ladd, 1968) from Funafuti Pleistocene or Holocene deposits.

#### ***Lagivala minusculus*, new species. Figure 80d–f.**

**Diagnosis.**—A very small species with narrow umbilicus, slightly elevated spire, numerous and crowded ribs, 1 parietal, and 1 sinuately twisted palatal.

Other *Lagivala* have much more widely open umbilici, two or three large parietals and three to five deeply recessed palatals. The singular palatal of *L. minusculus* immediately separates it from any of the *Vatusila* with reduced barrier number.

**Description.**—Shell very small, with  $3\frac{3}{4}$  tightly coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending slightly more rapidly, spire protrusion about  $\frac{1}{6}$  body whorl width, H/D ratio 0.404. Apical whorls  $1\frac{1}{2}$ , sculpture of 10 fine spiral cords, whose interstices are about 3–5 times their width. Postnuclear whorls with narrow, prominent, sharply defined, slightly sinuately protractive radial ribs, 121 on the body whorl, whose interstices usually are less than twice their width. Ribs/mm. 24.9. Microsculpture of very fine radial riblets, 2–4 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Sutures distinctly channelled after embryonic whorls, whorls strongly rounded above, moderately compressed laterally and on basal margin. Umbilicus relatively narrow, U-shaped, slightly and regularly decoiling, contained 5.22 times in the diameter, margins rounded. Color light reddish yellow-horn, no flammulations. Aperture ovate, compressed laterally and slightly on basal margin, inclined about 10° from shell axis. Parietal wall with single medial, high, bladeliike barrier, slightly twisted upward posteriorly, weakly expanded above, extend-

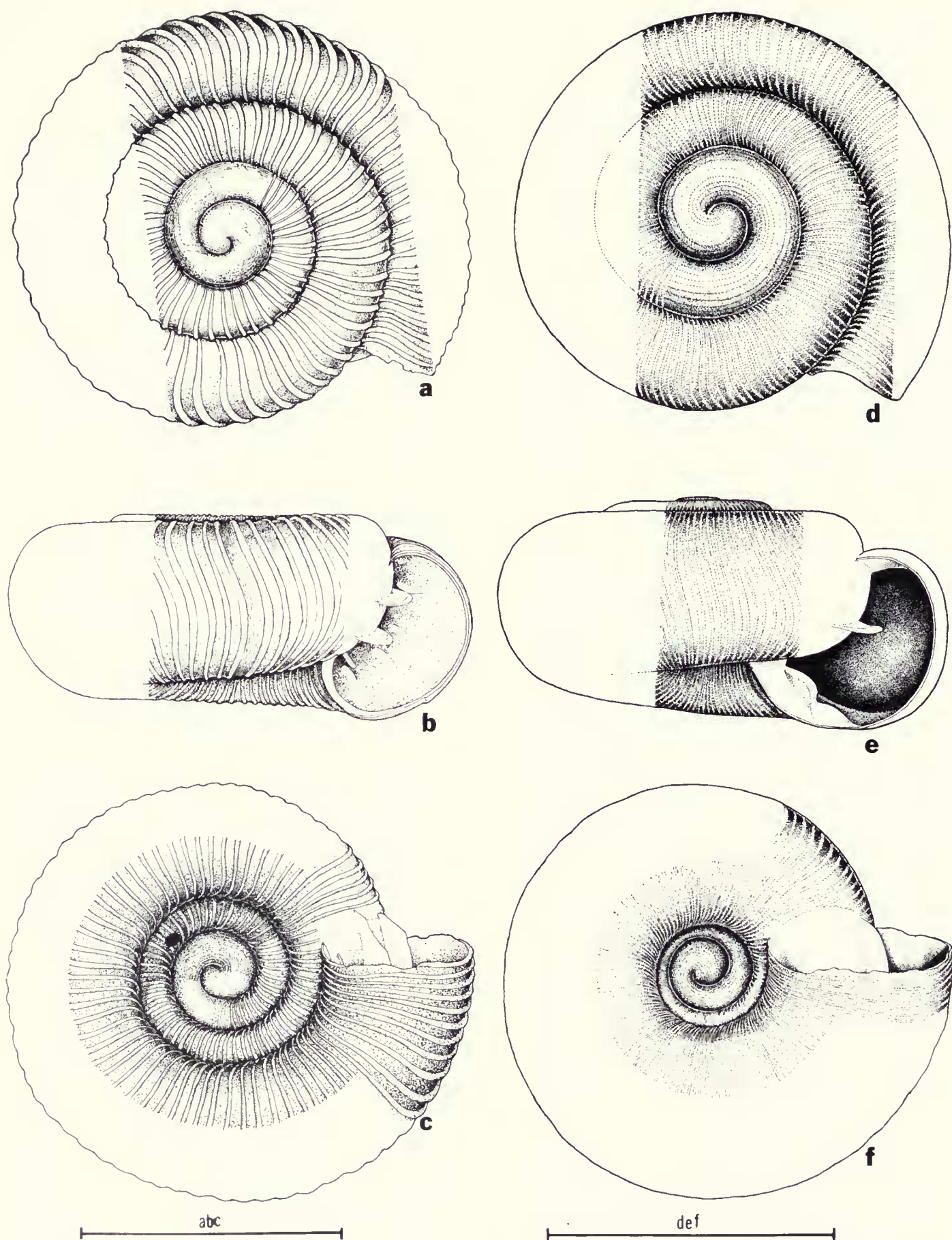


FIG. 80. **a–c**, *Lagivala vivus*, new species. Station 54, Telenaua, west of Suva, Viti Levu, Fiji. Holotype. BPBM 178598; **d–f**, *Lagivala minusculus*, new species. Nangava Island, Viti Levu, Fiji. Holotype. BPBM 179255. Scale lines equal 1 mm. (MM).



ing posteriorly beyond line of vision, without noticeable descension until just before anterior end. Outer wall with a single moderately elevated, bladeliike barrier, posteriorly at line of vision on columellar wall, anteriorly twisting down onto basal margin, reaching lip edge with sharp anterior descension, buttressed on outer side by a thick, tapering callus. Both barriers minutely serrated above. Height of holotype 0.63 mm., diameter 1.55 mm.

**Holotype.**—Fiji: Nangava Island, 1½ miles south of Viti Levu, near Namuka Island, at 210 ft. elevation. Collected under dead *hau* leaves by Yoshio Kondo on September 20, 1938. BPBM 179255.

**Range.**—Nangava Island, south of Viti Levu, Fiji.

**Remarks.**—Inclusion of this species in *Lagivala* is based upon the channeled suture (also in *L. macroglyphis* and *L. microglyphis*), shape of the parietal barrier (as in *L. vivus* and *L. davidi*), and general similarity of the columellar-palatal barrier to the third parietal in *L. vivus* (fig. 80b). The absence of any palatal barriers, narrow umbilicus, much more crowded and narrower ribbing, plus the peculiar termination of the columellar-palatal differ from the *Lagivala* pattern. It is quite possible that *L. minusculus* represents a distinct lineage and should be generically separated. Without more specimens and material for dissection I prefer to include it in *Lagivala*.

***Lagivala macroglyphis* (I. Rensch, 1937). Figure 81d–f.**

*Ptychodon macroglyphis* I. Rensch, 1937, Arch. f. Naturgesch., n. f., 6 (4), p. 592, fig. 36 right—Karlei, Malkong, and Matong, New Britain, Bismarck Archipelago.

**Diagnosis.**—Shell minute, diameter 1.64–1.89 mm. (mean 1.73 mm.), with 4¼–4% rather tightly coiled whorls. Apex and early spire flat or slightly depressed to barely elevated, last whorl descending much more rapidly, spire protrusion slightly more than ½ body whorl width, H/D ratio 0.539–0.580 (mean 0.553). Apical whorls 1%–1¼, sculpture of 11–12 fine spiral ribs whose interstices are about twice their width. Postnuclear sculpture of large, high, vertically sinuated radial ribs, 51 and 74 on 2 adult examples, whose interstices are 3–5 times their width. Ribs/mm. 9.86–12.46 (mean 11.16). Microsculpture a lattice of very fine, almost coequal spiral and radial riblets, 6–10 between each pair of major ribs. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.00–2.08 times (mean 2.03) in the diameter, margins distinctly shouldered, inner walls flattened, sutures strongly channeled with part of parietal wall detached. Sutures channeled above, whorls strongly rounded above and on basal margin with evenly rounded, strongly compressed laterally on outer margin, umbilical margin shouldered. Color partly leached from shell, a reddish yellow tint remaining. Aperture compressedly ovate, strongly rounded above and below, markedly compressed laterally, lying parallel to shell axis. Parietal barriers 2, extending posteriorly almost to line of vision: upper a high, thin blade with abrupt anterior descension, becoming thickened above on posterior 8th with slight downward twist or weakly bifid; lower parietal with anterior 8th a high threadlike ridge, abruptly becoming equal in height to upper parietal, greatly thickened, expanded and elevated above on posterior quarter. Columellar wall with single bladeliike barrier situated just below parietal-columellar margin on detached parietal wall, identical in form to 2nd parietal, but only half as high and extending not as far anteriorly. Palatal wall with 5 thin, deeply recessed, very short, crescentic ridges situated opposite posterior end of parietal barriers: 1st palatal basal in position, a very small, short crescent; 2nd a high crescentic barrier, weakly expanded above, whose apex lies opposite columellar; 3rd slightly lower than 2nd, situated subperipherally and directly opposite lower parietal; 4th equal in size to 3rd, situated opposite upper parietal; 5th smaller

than 1st, a tiny short, low barrier near upper palatal margin, occasionally absent. All barriers minutely serrated above.

The sympatric *Lagivala microglyphis* (fig. 81a–c) differs from *L. macroglyphis* (fig. 81d–f) in having a distinctly narrower umbilicus, lower H/D ratio, finer and more crowded radial ribs, plus slightly smaller average size. *Lagivala vivus* from Fiji lacks the partly detached parietal wall and thus has three parietals. It also has six palatals and a slightly depressed apex and spire.

**Holotype.**—Karlei, Weiten Bucht, New Britain, Bismarck Archipelago. Collected by Schneider. ZMB.

**Range.**—Karlei, Malkong, and Matong, New Britain, Bismarck Archipelago.

**Material.**—New Britain: Karlei (81 specimens, ZMB, FMNH 146021); Malkong-Bach, Karlei (25 specimens, ZMB); Matong (1 specimen, ZMB).

**Remarks.**—*Lagivala macroglyphis* has several unusual features produced by partial separation of the postnuclear whorls during growth. On the spire (fig. 81d) this is evidenced by deep channeling of the sutures that are partly filled by periostracal material in fresh examples. In the umbilicus (fig. 81f) there is the same partial detachment of the parietal wall seen in the Marquesan *Planudonta* (Solem, 1976a, figs. 146, 149). The upper portion of each umbilical volution lacks shell sculpture. This results from simple detachment of the parietal callus. At the same time, the 3rd parietal barrier of *L. vivus* has been lowered to occupy the “columellar wall.” It is, of course, completely homologous with the parietal and is called a columellar here only to facilitate identification by nonspecialists. At its anterior end there is a pronounced tendency for a distinct upward angling of the barrier to the functional columellar-parietal margin.

*Lagivala vivus* (fig. 80a–c) lacks the whorl detachment, has a narrower umbilicus, lower H/D ratio, a flat spire, and an additional palatal lamella. In size and sculpture it is quite similar.

***Lagivala microglyphis* (I. Rensch, 1937). Figure 81a–c.**

*Ptychodon microglyphis* I. Rensch, 1937, Arch. f. Naturgesch., n. f., 6 (4), p. 591, fig. 36 left—Karlei, Weiten Bucht, New Britain, Bismarck Archipelago; Solem, 1957, Fieldiana: Zoology, 42 (1), p. 7.

**Diagnosis.**—Shell minute, diameter 1.55–1.74 mm. (mean 1.63 mm.), with 3¼–4 rather tightly coiled whorls. Apex and early spire flat to barely protruding, last ½–¾ of body whorl descending a little to much more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.425–0.457 (mean 0.434). Apical whorls 1½, sculpture of 11 prominent spiral cords in only unworn examples. Postnuclear whorls with prominent, rounded, slightly protractively sinuated radial ribs, 86–101 (mean 95.5) on the body whorl, whose interstices are 1–3 times their width. Microsculpture of very fine radial riblets, 5–8 between each pair of major ribs, crossed by coequal spiral riblets. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.41–2.61 times (mean 2.54) in the diameter, margins rounded. Sutures deep, very weakly channeled, whorls strongly rounded above and on basal margin, nearly evenly rounded on outer margin with very slight lateral flattening above and below periphery. Color reddish yellow-horn without darker markings. Aperture subovate,



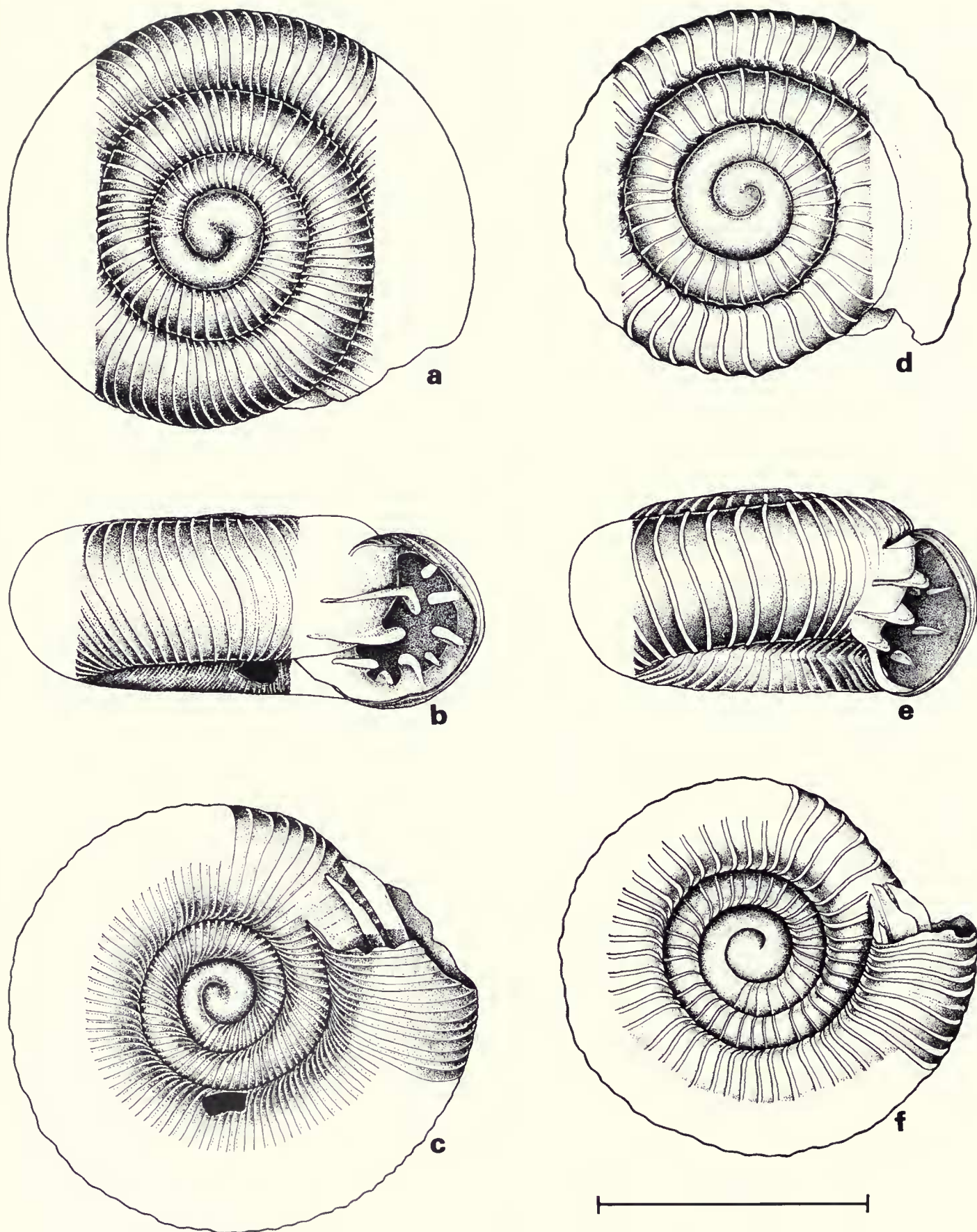


FIG. 81. **a–c**, *Lagivala microglyphis* (Rensch). Karlei, New Britain, Bismarck Archipelago. Paratype. FMNH 146022; **d–f**, *Lagivala macroglyphis* (Rensch). Karlei, New Britain, Bismarck Archipelago. Paratype. FMNH 146021. Scale line equals 1 mm. (SH).



strongly rounded above and at basal margin, evenly rounded elsewhere with slight lateral flattening, inclined about 20° from shell axis. Parietal barriers 2, extending posteriorly to line of vision: upper high and blade-like with very sharp anterior descension, slightly twisted upward, posterior third to quarter varying from bifid to with sharp downward deflection of greatly accentuated expanded portion; lower parietal a more rounded ridge with very gradual descension over anterior third, becoming higher, slightly bulbous on top, and twisted upward on posterior third. Columellar wall with single, bluntly rounded, moderately recessed, crescentic barrier extending posteriorly about 1/4 whorl with gradual anterior descension across top of columellar callus, slightly twisted upward over anterior third. Palatal wall normally with 5 deeply recessed, short, and crescentic barriers situated opposite posterior end of parietal barriers: lower palatal basal in position, a short crescent, slightly bulbous above, less than 2/3 height of next barrier; 2nd palatal high and crescentic, slightly bulbous above, pointing toward upper margin of lower parietal; 3rd palatal slightly smaller than 2nd, subperipheral, pointing between parietal barriers; 4th palatal equal in size to 2nd, slightly supraperipheral in position, situated opposite edge of upper parietal; 5th palatal equal in size to 1st, situated midway between 4th palatal and parietal-palatal margin. Occasionally only 3 palatals are present, and an accessory trace may be present between various lower palatal pairs. Expanded upper portions of each barrier with minute crystalline barbs.

*Lagivala microglyphis* has many more radial ribs, a much lower H/D ratio, fewer whorls (table XL), and a more rounded whorl contour than does the sympatric *L. macroglyphis* (fig. 81d-f). In *L. vivus* (fig. 80a-c) there are three parietals and no columellar, the latter in both *L. macroglyphis* and *L. microglyphis* being a descended third parietal.

*Holotype*.—Karlei, Weiten Bucht, New Britain, Bismarck Archipelago. Collected by Schneider. ZMB.

*Range*.—Karlei, New Britain, Bismarck Archipelago.

*Material*.—Karlei (5 specimens, ZMB, FMNH 146022).

*Remarks*.—The five paratypes showed some barrier variation. A small accessory crescentic barrier lies between the second and third palatals of the largest specimen; one adult had the first and fourth palatals missing, with the second and third grossly thickened; a juvenile lacked the first and fourth palatals, with no thickening of the second and third palatals. The tendency toward loss of two palatals provides a link to the condition seen in *L. davidi*.

Suture channeling in *L. microglyphis* is greatly reduced, and there is no indication of sculptural change in the umbilicus caused by parietal wall descension, despite the position of the columellar barrier. The sculpture is much finer than in other *Lagivala*, except for the unusual *L. minusculus*. Whether *L. microglyphis* is an advanced or a generalized species cannot be determined without additional material for study and dissection.

### *Lagivala demani* (Tapparone-Canefri, 1883).

*Patula demani* Tapparone-Canefri, 1883, Ann. Mus. Civ. Stor. Nat., Genova, 19, pp. 95–96, 300, pl. 2, figs. 13–15—Vokan, Aru Islands; van Benthem Jutting, 1962, Ann. Mus. Civ. Stor. Nat., Genova, 73, p. 5.

*Helix demani* (Tapparone-Canefri), Tryon, 1887, Man. Conchol., (2) 3, pp. 26–27, pl. 4, figs. 39–41.

*Nesophila demani* (Tapparone-Canefri), Boettger, 1922, Abh. Senckenb. Naturf. Ges., 35 (4), pp. 373–374, pl. 21, fig. 5.

*Beilania demani* (Tapparone-Canefri), Solem, 1958, Arch. f. Mollusk., 87 (1–3), p. 22; van Benthem Jutting, 1964, Nova Guinea, Zool., 26, pp. 11–13 (partly)—localities on Biak.

*Ptychodon demani* (Tapparone-Canefri), van Benthem Jutting, 1958, Nova Guinea, Zool., 9 (2), p. 327—Waima, Misool.

*Diagnosis*.—Shell relatively large, diameter 1.73–2.07 mm. (mean 1.90 mm.), with 3 3/4–4 1/2 tightly coiled whorls. Apex and spire slightly and evenly elevated to moderately depressed below level of penultimate whorl, often flat, body whorl descending much more rapidly, spire protrusion at most 1/4 body whorl width, H/D ratio 0.416–0.518 (mean 0.448). Apical sculpture of 10–14 (mean 12.1) very fine spiral cords, whose interstices are about 3 times their width. Postnuclear whorls with prominent to very prominent, high, sharply defined, usually slightly protractive radial ribs, 56–106 (mean 79.0) on the body whorl, whose interstices are 1 1/2–5 times their width. Ribs/mm. 9.85–19.4 (mean 13.1). Microsculpture of fine radial riblets, 3–13 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets, no secondary spiral cording. Umbilicus very widely open, V-shaped, regularly decoiling, contained 2.48–3.03 times (mean 2.64) in the diameter, margins rounded. Sutures deep, whorls strongly rounded above and on baso-columellar margin, outer margin varying from markedly compressed laterally to almost evenly rounded with slight lateral compression above periphery. Aperture subcircular to compressedly ovate, inclined about 5°–10° from shell axis. Parietal barriers normally 2 (only one known population with 3), high, extending posteriorly 3/16–1/4 whorl: upper very high and slender with abrupt anterior descension, posterior quarter often slightly more elevated with a downward twist to elevated portion; 2nd usually equal in height on crescentic posterior 3rd, which may be slightly twisted upward, middle 3rd slightly lower and less expanded or descending, with gradual descension over anterior 3rd until just before termination slightly in front of upper parietal; 3rd, when present, about 1/2–2/3 height of 2nd, just above parietal-columellar margin. Columellar wall without any barrier (Biak and West Irian), with a very small and deeply recessed, ridgelike trace (Biak), a medium-size barrier (Ambon and Aru Islands), or with barrier almost equal in size to 2nd parietal (Timor). Palatal barriers 3 or 4, rarely absent, deeply recessed, variable in size and position, crescentic and short to elongated lamellar ridges: 1st through 3rd on basal to outer lip, with 3rd just above periphery and opposite upper parietal, sometimes shifted lower on outer wall; 4th, when present, midway between 3rd palatal and palatal-parietal margin.

*Lagivala demani* differs from the Fijian *L. vivus* and the two Bismarck species in its reduced number of palatal barriers, generally lower H/D ratio, and slightly greater size. *Lagivala macroglyphis* is much more widely umbilicated, has a distinctly protruded spire, and is very strongly compressed laterally on the whorl margin. *Lagivala microglyphis* has finer radial ribbing, is smaller, the body whorl has only slight lateral compression, and the aperture is inclined about 20° from the shell axis. *Lagivala vivus* always has a 3rd parietal and 6 palatals.

*Description*.—Shell minute, with 3 3/4 moderately tightly coiled whorls. Apex and spire slightly emergent, body whorl descending only a little more rapidly, H/D ratio 0.454. Surface of shell heavily encrusted with dirt and fungal growth so that sculptural details are obscured. Size and position of major ribs as in "Diagnosis" cited above. Umbilicus broadly V-shaped, widely open, regularly decoiling, contained 2.54 times in the diameter. Apertural lip badly broken, obscuring shape of aperture, sutures filled with extraneous matter. Aperture showing only anterior edges of the 2 parietal barriers,

otherwise choked with dirt and fungal hyphae. Height of lectotype 0.74 mm., diameter 1.63 mm.

*Lectotype*.—Aru Islands: Wokan. Collected by O. Beccari. MSNG.

*Range*.—Ambon, Timor, Wokan in the Aru Islands, Misool, Biak off West Irian, and coastal areas of West Irian. Possibly Celebes.

*Paratypes*.—MSNG, SMF 4678.

*Material*.—Ambon (1 specimen, ZMA collected October 11–13, 1949, by M. A. Lieftinck). Timor: Araki-Vlakte (5 specimens, FMNH 150775, ZMA collected April 12, 1950, by B. Polak). Aru Islands: Wokan (5 specimens, MSNG, SMF 4678). Misool: Waima (6 specimens, FMNH 150774, ZMA collected September 13–14, 1948 by M. A. Lieftinck). Biak: Kombai (00° 46', 135° 58') (12 specimens, ZMA, RNHL); Korim (00° 55', 136° 04') (10 specimens, FMNH 150776, RNHL); Station G-65, Saba (1 specimen, RNHL); Station G-34, Owi, South Biak (1 specimen, RNHL); Station G-30, Bosnik (1 specimen, RNHL). West Irian: Ugar, Kokas District (1 specimen, RNHL collected June 6, 1953); Sarmi (01° 52', 138° 44') (2 specimens, ZMA collected December, 1962, by G. J. M. Gerrits).

*Remarks*.—In the type lot of *Lagivala demani* there were five examples of this species and a single *Discocharopa aperta* (Möllerndorff). Tapparone-Canefri's original figures show an extremely widely umbilicated shell without trace of apertural barriers. Although the *Lagivala* were all juvenile and had the aperture choked with dirt so that only the tips of the parietals were visible, I suspect that, despite no mention of the barriers, the description was based on the *Lagivala* and the figures on the *Discocharopa*. Boettger (1922) illustrated one specimen from the type lot with the parietals and depressed spire. I prefer to use the name in this sense rather than to adopt the *Discocharopa* as type, since its reduced sculpture and elevated spire agrees more with the type figures. Tapparone-Canefri (1883, p. 300) indicated in the explanation of the plates that the sculpture was omitted. The very fine ribs of the *Discocharopa* could have been overlooked much more easily than the coarse ribbing of the *Lagivala*. Recently, van Benthem Jutting (1962, p. 5) indicated that the lectotype was the "shell figures pl. 2, fig. 13–15." There is little agreement between the lectotype and the figures.

Unfortunately, most available material was juvenile. Only 12 of the Biak examples from Kombai, Korim, and Saba plus one shell from Misool showed adult shell features. Because of the barrier variation, changes in spire elevation and ribbing and variation data for several sets of adults and juveniles are summarized in Table XLI. Size differences should be ignored, because the sets are not comparable in age composition. Since umbilical decoiling is regular in this species and the spire is normally flat or depressed, both D/U and H/D ratios would be little affected by the change from juvenile to adult growth. The very slightly increased H/D ratio for the Timor shells is attributable

to the slightly elevated spire in that population. Shells from Misool are more narrowly umbilicated, whereas those from Korim, Biak, have a lower H/D ratio, possibly as a correlative with the more depressed apex and spire of that population. Rib counts vary widely, but the more critical factor of rib spacing shows agreement between the samples. Timor shells do have more prominent ribs, but there is only a slight decrease in rib spacing that is not statistically significant. Misool shells have narrower and thus more numerous and slightly more crowded major ribs (mean ribs/mm. 13.83) than other sets. Measured differences are thus minor.

Changes in spire protrusion and apertural barriers are much more significant. In the types from Wokan, Aru Islands, the spire is barely elevated, the columellar barrier is high but deeply recessed, and the three palatals are situated in normal position, deeply recessed, short and high. Juveniles from Timor in addition to the enlarged radial ribbing have the spire and apex distinctly elevated, the columellar barrier is half to two-thirds as high as the second parietal and extends to the top of the columellar callus with gradual anterior descension, plus four palatals. The lower three are high and crescentic, with the first at the baso-lower palatal margin, the second pointing toward the lower parietal top edge, and the third opposite and nearly touching the upper parietal. A much smaller and lower fourth palatal lies one-third of the way between the third palatal and the palatal-parietal margin. One individual has an accessory cordlike trace at the baso-columellar margin, more deeply recessed than the first palatal and much shorter. All specimens from Biak have a flat or noticeably depressed spire, the columellar reduced to a threadlike or ridged lamellar trace visible only by extreme tilting of the aperture, and the three palatals longer, much lower, with the second situated distinctly above the second parietal level, and the third sometimes split into two parts. The Misool examples have the spire flat or very slightly depressed, no trace of any columellar barrier, and the position of the palatals altered so that the first palatal lies at the baso-columellar margin, the second at the baso-lower palatal margin, and the third pointing between the first and second parietals. In size these palatals are intermediate between those of the Biak and Timor examples. Their downward shift in position probably reflects adjustments to the columellar barrier loss and serves to restore balanced narrowing of the aperture. The broken and worn individual from Ambon has a medium-sized columellar barrier, the palatals shifted as in the Misool shells, and the spire very slightly elevated. Two shells from Sarmi, West Irian, have a third barrier on the lower edge of the parietal wall and equal in height posteriorly to the second parietal. Its anterior descension is very gradual and terminates behind the end of the first parietal. There is no columellar barrier as such. One shell has the typical short and crescentic, deeply recessed three palatals, the other lacks any



TABLE XL1. - LOCAL VARIATION IN *LAGIVALA DEMANI*.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER
Sarmi, W. Irian ZMA	2	65.5±10.53 (55-76)	13.0±1.32 (11.68-14.31)	0.76±0.049 (0.71-0.81)	1.60±0.099 (1.50-1.69)
Kombai, Biak ZMA, RNHL	5	75.5±4.01 (56-106)	13.1±0.66 (9.85-19.39)	0.86±0.032 (0.76-0.93)	1.86±0.080 (1.66-2.06)
Korim, Biak RNHL	7	70.1±3.37 (56-85)	12.3±0.47 (9.88-13.87)	0.79±0.017 (0.72-0.86)	1.82±0.042 (1.63-1.96)
Saba, Biak RNHL	1	----	----	0.95	2.07
Waima, Misool ZMA	5	71.8±6.65 (56-87)	13.8±0.41 (12.92-14.85)	0.75±0.044 (0.66-0.90)	1.61±0.101 (1.38-1.97)
Araki-Vlakte, Timor ZMA	4	54.5±2.53 (47-58)	12.7±0.54 (11.33-13.68)	0.66±0.017 (0.63-0.71)	1.37±0.028 (1.32-1.45)
Wokan, Aru SMF 4678, MSNG	5	57.7±0.33 (57-58)	13.0±0.61 (12.31-14.20)	0.68±0.022 (0.64-0.74)	1.45±0.056 (1.30-1.63)
Ambon ZMA	1	50	10.2	0.74	1.56

	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO
Sarmi	0.475±0.0014 (0.473-0.476)	4 1/8	0.66±0.033 (0.63-0.69)	2.41±0.030 (2.39-2.45)
Kombai	0.465±0.0134 (0.443-0.518)	4 1/4 (4-4 1/2)	0.69±0.046 (0.58-0.81)	2.71±0.086 (2.55-3.03)
Korim	0.435±0.0040 (0.416-0.448)	4 (3 1/2-4 1/4)	0.71±0.020 (0.64-0.79)	2.55±0.021 (2.48-2.63)
Saba	0.460	4 1/2	0.82	2.52
Waima	0.463±0.0118 (0.455-0.476)	3 1/2-(3 1/8-3 3/4)	0.54±0.040 (0.41-0.66)	2.99±0.100 (2.81-3.36)
Araki	0.485±0.0100 (0.475-0.488)	-----	0.51±0.019 (0.46-0.54)	2.66±0.076 (2.49-2.86)
Wokan	0.468±0.0099 (0.438-0.493)	3 1/2-(3 1/4-3 7/8)	0.55±0.031 (0.48-0.64)	2.67±0.054 (2.53-2.78)
Ambon	0.473	-----	0.63	2.50

trace of palatals. Whorl contours vary with the ribbing, the Sarmi and Misool shells having the body whorl markedly compressed laterally, the Biak shells showing only slight lateral compression, and the Timor shells having a subcircular body whorl contour with some lateral compression above the periphery. Reduction of the columellar barrier correlates with increased lateral compression of the body whorl.

Recognizably different populations exist, and the pattern of variation in many Wallacean animal groups strongly suggests subspeciation has occurred. With only single collections of mainly juvenile individuals from widely scattered areas I prefer not to give nomenclatural recognition to these populations. Variational data summarized above and in Table XLI should enable interpretation of variation in additional populations but are not sufficient for description of subspecific units.

The wide range of this species, extending as far west as Timor, Ambon, and Misool, makes it quite

plausible that *Beilania inopina* Preston, 1913, from Beilan-Beilan Island north of Obi is a member of this complex. Reasons for not including it at this time have been given above (p. 184).

A single worn and broken shell from Tjamba Pass, near Makassar, South Celebes, was located in a set of *Discocharopa aperta*. It may be an undescribed species of *Lagivala* or represent a population of *L. demani* in which the palatals are very close to the lip.

#### Genus *Vatusila*, new genus

Shell relatively small to very small, with 3½-5 normally to rather tightly coiled whorls. Apex and spire flat (*eniwetokensis*) to rather strongly elevated (*nayauana*), body whorl usually descending much more rapidly. Apical sculpture of 8-12 fine, but prominent spiral cords. Postnuclear sculpture of crowded to widely spaced radial ribs, strong secondary spiral cording in all but *niueana* (weakened) and *vaitupuensis* (absent). Umbilicus rather widely open, narrowed in *kondoi*. Periphery rounded, whorls slightly to strongly flattened laterally above periphery. Color flammulations, when present, not zigzagged, following lines of growth. Parietal wall with 2 barriers, 1

bifurcated barrier, or greatly reduced single barrier. Columellar wall with or without recessed, low ridge. Palatal barriers varying from 0–3, broadly expanded (*tongensis*) down to a low, broad remnant callus (*niueana*). Anatomy mostly unknown, penis in *tongensis* differing from *Sinployea* only in accentuation of semicircular pilasters forming vergic papilla.

*Type species.*—*Vatusila tongensis*, new species.

Despite the rather widely different appearance of the sculpture and large size range, I have no hesitation in considering these species congeneric. The two small species, *V. kondoi* (fig. 82a–c) and *V. nayauana* (fig. 82d–f) from the Lau Group, and *V. eniwetokensis* (fig. 85e–f) from the Miocene of Eniwetok, agree in shell microsculpture, although not in parietal barrier size or character of major ribbing. The larger *V. tongensis* (fig. 83a–c) from Eua has the microsculpture of this group and agrees in parietal barrier shape with the fossil. Comparison of the figures shows that a callus connecting the second and third palatals, elaboration of the first palatal, and loss of the columellar from *V. kondoi* would duplicate the outer lip barriers in *V. tongensis*. Although no direct linear relationship between these species should be implied, all the above species could be derived from a common model. *Vatusila vaitupuensis* (fig. 85a–d) and *V. niueana* (fig. 83d–f) would represent successive stages in barrier reduction from a *V. tongensis* barrier stage, although they agree more with *V. eniwetokensis* in major rib spacing. They differ in having modified secondary spiral sculpture or none (*vaitupuensis*).

It is significant that those with the widely spaced major sculpture, *V. tongensis*, *V. kondoi*, and *V. nayauana*, are from a central area, whereas those with more average sculpture, *V. niueana*, *V. vaitupuensis*, and *V. eniwetokensis*, have a fringing distribution around this core. I suspect that more species of this group will be discovered in Fiji and Tonga when additional collections become available.

Comparisons with other genera are unsatisfactory because so little anatomical data were available. The penis of *Vatusila tongensis* (fig. 84a–b) represents a rather minor change from the pattern seen in *Sinployea*. Without more complete material for study, the closeness of this relationship will remain uncertain. The small species with heavier barriers show considerable sculptural modification from the pattern of *Sinployea*, whereas one of the larger species, *V. niueana*, can be mistaken for that genus very easily. Progressive reduction in aperture barriers with increased size is common in the Endodontidae, but this cannot be postulated for *Vatusila*, because the sizes of *V. tongensis*, *V. vaitupuensis*, and *V. niueana* are essentially identical. Species of *Lagivala* have much simpler structure to the parietal barriers; their palatals are short, simple, and very deeply recessed. They differ in both microsculpture and whorl contours and seem to be a group paralleling the structures of *Vatusila*, but of different origin. *Microcharopa* (fig. 33a–c) is smaller, has greatly modified apical shell sculpture, and lacks apertural barriers. *Graeffedon* (figs. 86, 88) is much,

much larger and has quite different palatal barriers (although the parietals have a similar structure to those found in *V. eniwetokensis*) and a very different anatomy (fig. 87a–d).

*Vatusila* is named after the Fijian tribe (located at the headwaters of the Sigatoka River) that killed and ate Rev. Thomas Baker, a Wesleyan missionary, on July 21, 1867.

### *Vatusila kondoi*, new species. Figure 82a–c.

*Diagnosis.*—Shell very small, diameter 1.68–1.84 mm. (mean 1.75 mm.), with 3½–3¾ normally coiled whorls. Apex and spire moderately elevated, slightly rounded above, last whorl descending much more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.500–0.610 (mean 0.552). Apical sculpture of 9–11 (mean 10.3) rather fine spiral cords. Postnuclear whorls with high, prominent, very widely spaced, strongly protractively sinuated radial ribs, 31–48 (mean 39.0) on the body whorl, whose interstices are 5–10 times their width. Ribs/mm. 5.51–8.06 (mean 7.04). Microsculpture of barely visible radial and spiral riblets, almost completely obscured by prominent and crowded secondary spiral cording. Umbilicus narrow, U-shaped, slightly and regularly decoiling, contained 4.12–5.40 times (mean 4.72) in the diameter, margins rounded. Sutures deep, whorls strongly rounded above, flattened laterally with a weak supraparipheral sulcus, basal margin evenly rounded and slightly compressed. Aperture ovate, inclined about 15° from shell axis. Parietal wall with single high barrier, extending ⅓–¾ of a whorl posteriorly, crescentic in outline with gradual anterior and posterior descension, usually flattened above on middle third, varying from slightly thickened medially to broadly bifid, with superior arm of barrier twisted upward. Columellar wall with low, broadly rounded, cordlike ridge, lying parallel to plane of coiling, reaching top of columellar callus, occasionally (5.6%) absent. Palatal barriers usually 3, sometimes (11.1%) only 2, short, moderately to deeply recessed within aperture: lower basal in position, crescentic, broadly rounded above; 2nd much lower and slightly shorter; 3rd slightly supraparipheral, longer, narrower, more deeply recessed bladelikey barrier with a very gradual anterior descension. Columellar and lower palatal walls with a rather thick callus.

*Vatusila kondoi* (fig. 82a–c) is smaller and has much smaller apertural barriers than the Eua Island *V. tongensis* (fig. 83a–c). *Vatusila nayauana* (fig. 82d–f) has a distinctly higher spire, more crowded radial ribbing, a wider umbilicus (table XLII), and reduced apertural barriers. *Vatusila eniwetokensis* (fig. 85e–f) has much more numerous and crowded radial ribs, two parietals, and a wider umbilicus.

*Description.*—Shell very small, with 3½ moderately loosely coiled whorls. Apex and spire moderately elevated, rounded above, last whorl descending rapidly, H/D ratio 0.558. Apical whorls 1¾, sculpture of 11 relatively prominent, narrow spiral ribs, partly eroded. Postnuclear whorls with widely spaced, protractively sinuated, narrow, rounded radial ribs, 34 on the body whorl, whose interstices are 5–10 times their width. Microsculpture of very fine, close-set radial ribs, crossing quite strong, relatively prominent secondary spiral cords. Microspiral sculpture barely visible. Major ribs beaded on top by crossing of spiral cords. Sutures moderately deep, whorls shouldered above, flattened laterally above periphery with slight basal flattening, a weak supraparipheral sulcus present. Umbilicus narrowly U-shaped, regularly decoiling, slightly constricted by expansion of basal lip, contained 4.72 times in the diameter. Color uniform light yellow-brown. Aperture ovate, strongly flattened above periphery, slightly so on base, inclined about 15° from the shell axis. Parietal wall with a single high barrier, extending about ¾ of a whorl, gradually descending anteriorly and posteriorly, broadly expanded above and bifid in center. Columellar barrier a broad, rounded, moderately prominent ridge, lying parallel to plane of coil-



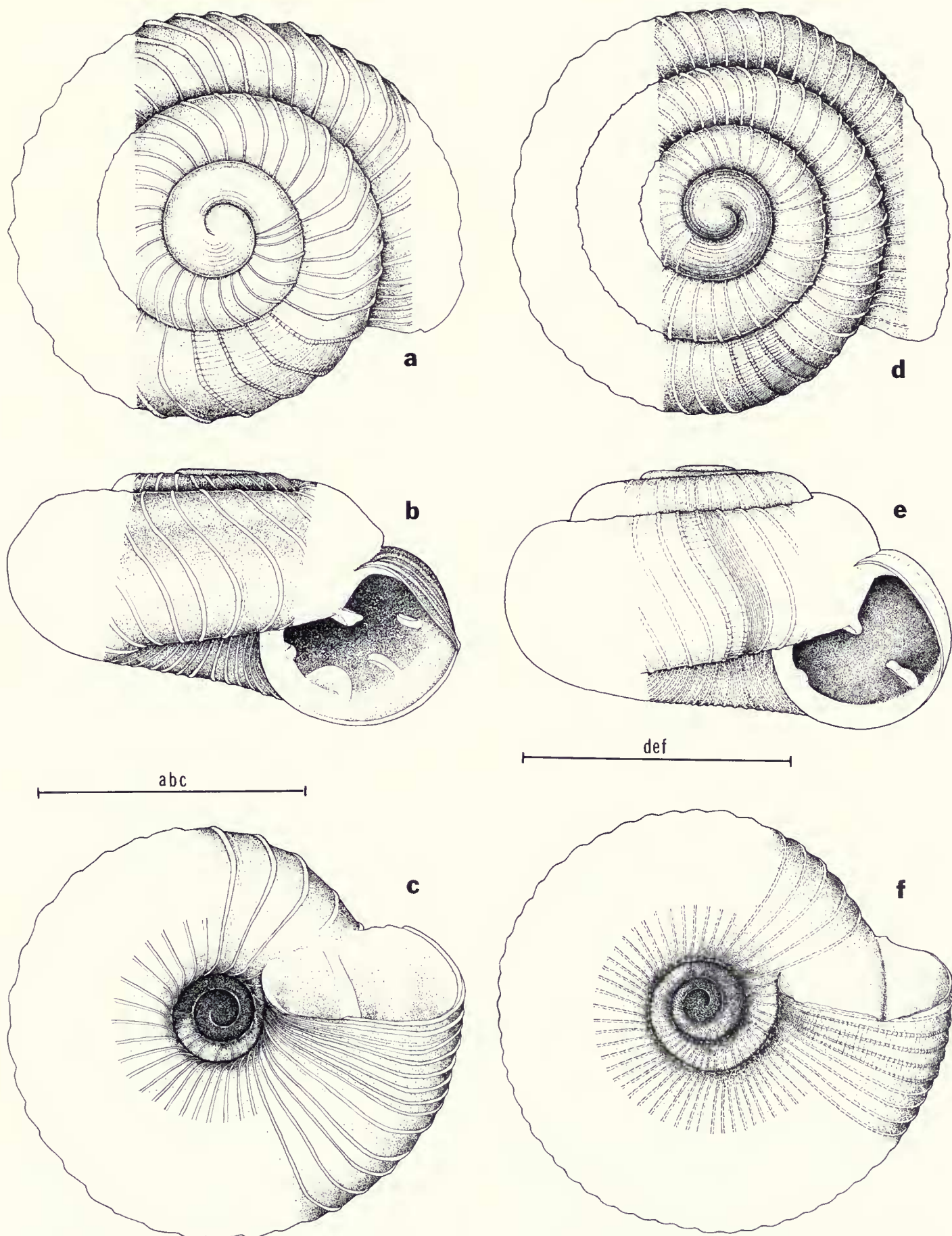


FIG. 82. **a-c**, *Vatusila kondoi*, new species. Station 101, Nayau, Lau, Fiji. Holotype. BPBM 180259; **d-f**, *Vatusila nayauana*, new species. Station 43, Nayau, Lau, Fiji. Holotype. BPBM 167232. Scale lines equal 1 mm. (MM).

TABLE XLII. — RANGE OF VARIATION IN VATUSILA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<i>kondoi</i>	56	39.0(31-48)	7.04(5.51-8.06)	0.97(0.86-1.05)	1.75(1.68-1.84)	0.552(0.500-0.610)
<i>nayauana</i>	42	51.0(48-54)	9.48(9.11-9.85)	0.95(0.87-1.02)	1.65(1.58-1.74)	0.573(0.552-0.608)
<i>eniwetokensis</i> (Ladd)	1	89	15.1	0.86	1.88	0.456
<i>tongensis</i>	20	61.0(52-72)	7.66(6.89-8.71)	1.36(1.13-1.72)	2.53(2.32-2.75)	0.538(0.472-0.650)
<i>vaitupuensis</i>	2	115	14.27	1.25	2.57	0.487
<i>niueana</i>	1	89	11.60	1.27	2.44	0.500

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<i>kondoi</i>	3 1/2+(3 3/8-3 7/8)	0.37(0.35-0.43)	4.72(4.12-5.40)	10.3(9-11)
<i>nayau.</i>	4-(3 5/8-4 1/8)	0.46(0.43-0.48)	3.61(3.43-3.69)	10.1(9-11)
<i>eniwe.</i>	3 1/2	0.53	3.56	12
<i>tonge.</i>	4 5/8-(4 1/4-5)	0.76(0.66-0.89)	3.31(3.00-4.00)	10.4(8-12)
<i>vaitu.</i>	4 1/2+	0.89	2.89	8
<i>niuea.</i>	4 1/4	0.66	3.70	10

	SPIRE ELEVATION	BODY WHORL WIDTH	SP/B <sup>WH</sup>	PR	C	P
<i>kondoi</i>	0.10	0.56	0.177	1 <sup>1</sup>	0-1	2-3
<i>nayau.</i>	0.17(0.13-0.23)	0.53(0.48-0.56)	0.310(0.260-0.420)	1	0-1	0-1
<i>eniwe.</i>	FLAT	0.61	FLAT	2	?	?
<i>tonge.</i>	0.20(0.16-0.30)	0.76(0.63-0.82)	0.270(0.200-0.375)	1 <sup>1</sup>	0	2 <sup>2</sup>
<i>vaitu.</i>	0.13	0.79	0.167	1	0	2
<i>niuea.</i>	0.13	0.76	0.174	1 (Reduced)	0	Callus

1. Bifid  
2. Enlarged laterally

ing, reaching top of columellar callus. Palatal barriers 3: lower reaching edge of moderate apertural callus, short,  $\frac{1}{16}$  whorl in length, a high, broadly rounded ridge; middle palatal slightly more deeply recessed, lower, narrower, an equally short threadlike ridge; upper slightly supraperipheral in position, a broad V-shaped ridge, short, with gradual anterior descension about as deeply recessed as middle palatal. All barriers minutely serrated above and on sides. Height of holotype 0.95 mm., diameter 1.71 mm.

**Holotype.**—Fiji: Lau Group, Nayau, Station 101,  $\frac{3}{4}$  mile north of Liku Village at base of a limestone cliff, 100 yd. inland at 30–500 ft. elevation. Collected in leaf litter by Yoshio Kondo on August 22, 1938. BPBM 180259.

**Range.**—Nayau, Lau Group, Fiji.

**Paratypes.**—Lau Group: Nayau,  $\frac{3}{4}$  mile north of Liku Village (Station 101) at base of a limestone cliff, 100 yd. inland at 30–500 ft. elevation (56 specimens, BPBM 180259).

**Remarks.**—The parietal barrier in *Vatusila kondoi* varies from a single lamellate ridge to a markedly bifid barrier as in the type (fig. 82b). The columellar barrier is often reduced in size, occasionally absent,

and the middle palatal may be absent. These variations are relatively minor and do not bridge the gap between the barriers of *V. kondoi* and *V. nayauana*. Differences in proportions (table XLII) are equally large, and I have no hesitation in placing them as distinct species.

Great pleasure is taken in naming this species after its collector, Dr. Yoshio Kondo.

**Vatusila nayauana**, new species. Figure 82d–f.

**Diagnosis.**—Shell very small, diameter 1.58–1.74 mm. (mean 1.65 mm.), with  $3\frac{3}{8}$ – $4\frac{1}{8}$  rather tightly coiled whorls. Apex and spire rather strongly elevated, sometimes rounded above, last whorl descending distinctly more rapidly, spire protrusion about  $\frac{1}{3}$  body whorl width, H/D ratio 0.552–0.608 (mean 0.573). Apical sculpture of 9–11 (mean 10.1) fine spiral cords, whose interstices are about 3 times their width. Postnuclear whorls with narrow, prominent, rounded, protractively sinuated radial ribs, 48–54 (mean 51.0) on the body whorl, whose interstices are 3–7 times their width. Ribs/mm. 9.11–9.85 (mean 9.48). Microsculpture of extremely fine radial and spiral riblets, obscured by much more prominent, rather crowded secondary spiral cords. Umbilicus rather widely open, broadly U-shaped, last whorl decoiling more rapidly, contained 3.43–3.69 times



(mean 3.61) in the diameter, margins rounded. Sutures deep, whorls strongly rounded above, slightly flattened laterally above periphery, with evenly rounded lower margins. Aperture ovate, inclined about  $10^\circ$  from shell axis. Parietal barrier a short, high, crescentic blade, extending posteriorly about  $\frac{1}{8}$  whorl, expanded and serrated above, with gradual anterior and posterior descension, medial in position. Columellar wall with (60%) or without (40%) a low, rounded cordlike ridge that barely reaches top of columellar callus. Palatal wall with (60%) or without (40%) a single, bladelike barrier, relatively low, strongly expanded and serrated above, with gradual anterior descension, moderately recessed, situated on middle of lower palatal margin.

*Vatusila nayauana* (fig. 82d-f) differs from *V. kondoi* (fig. 82a-c) in its fewer and smaller apertural barriers, much wider umbilicus, more protruded spire, more crowded radial ribs, and greater H/D ratio (table XLII). *Vatusila eniwetokensis* (fig. 85e-f) has two parietals, much more numerous and crowded ribbing, plus a flat spire. *Vatusila tongensis* (fig. 83a-c) is much larger and has grossly developed apertural barriers.

**Description.**—Shell very small, with slightly over 4 rather tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, H/D ratio 0.608. Apical whorls  $1\frac{1}{2}$ , sculpture of 11 narrow spiral ribs, whose interstices are about 3 times their width. Postnuclear whorls with protractively sinuated, widely spaced, prominent, rounded radial ribs, 48 on the body whorl, whose interstices are 3–5 times their width, becoming more crowded on the last half of body whorl. Microsculpture of very fine and crowded, inconspicuous radial riblets and lower, much more crowded spiral riblets, crossing stronger, rather widely spaced spiral cords. Major ribs finely beaded above by crossing of spiral cords. Sutures relatively deep, whorls strongly rounded above, slightly flattened laterally above periphery. Umbilicus open, broadly U-shaped, last whorl decoiling more rapidly, contained 3.64 times in the diameter. Aperture circular, inclined about  $10^\circ$  from the shell axis with a moderately prominent basal callus. Parietal wall with a short barrier extending about  $\frac{1}{8}$  whorl, broadly rounded and ridgelike. Columellar wall with a small, deeply recessed, cordlike tubercle. Palatal wall with a subperipheral, broadly rounded ridgelike barrier, moderately recessed, expanded above, extending about  $\frac{1}{16}$  of a whorl. Major palatal and parietal minutely serrated above and on sides. Height of holotype 1.02 mm., diameter 1.68 mm.

**Holotype.**—Fiji: Lau Group, Nayau, northwest coast, Station 43, Nauko, hillside  $\frac{1}{2}$  mile inland at 250 ft. elevation. Collected dead at the base of a limestone cliff by H. S. Ladd on August 13, 1934. BPBM 167232.

**Range.**—Nayau, Lau Group, Fiji.

**Paratypes.**—Lau Group; Nauko, hillside,  $\frac{1}{2}$  mile inland (Station 43) at 250 ft. elevation (42 specimens, BPBM 167232).

**Remarks.**—Although *Vatusila nayauana* can be derived from *V. kondoi* by a combination of barrier reduction, greater spire protrusion, rib crowding, and umbilical widening, these changes are not correlated. Hence specific-level recognition is warranted.

The exact relationship of the type localities is uncertain. *Vatusila nayauana* was taken on the northwest coast of Nayau, either at or on the way to Ladd's geological station L502-L504 (Ladd & Hoffmeister, 1945, pp. 86, 190). *Vatusila kondoi* was taken "three-quarters mile north of Liku Village." The latter is located approximately in the middle of the southwest coast of the island. Although this locality is 100 yd. inland, Ladd's station was cited as  $\frac{1}{2}$  mile inland.

Hence, regardless of the relative shore proximity of the sites, they are separated at a minimum by about 700–800 yd. Thus the snails are isolated colonies. Only five examples were adult. Most of the rest had the aperture clogged with debris. Hence the proportion of specimens that lack the columellar and palatal barriers may be altered considerably when new collections are available.

***Vatusila eniwetokensis*** (Ladd, 1958). Figure 85e-f.

*Ptychodon eniwetokensis* Ladd, 1958, J. Paleont., 32 (1), p. 190, pl. 30, figs. 9–12—Drill hole K-1B at 820–831 ft. depth, Engebi Islet, Eniwetok Atoll, Marshall Island (Miocene g).

**Description.**—Shell very small, probably with 4 whorls when complete (only  $3\frac{1}{2}$  remaining). Apex barely emergent, spire flat, last whorl descending more rapidly, H/D ratio of remnant 0.456. Apical whorls  $1\frac{1}{2}$ , sculpture of 12 fine spiral ribs. Lower whorls with crowded, prominently narrow, protractively sinuated radial ribs, 89 on last complete whorl, whose interstices are 2–3 times their width. Microsculpture with 2 elements: a greatly reduced microlattice visible on a few areas under  $96\times$  magnification and a much more prominent sculpture of rather widely spaced spiral cords (fig. 85f). Sutures channeled above on postapical spire and body whorl, whorls strongly rounded above, slightly flattened laterally above and below rounded periphery, with evenly rounded baso-umbilical margin. Very faint brownish yellow cast to entire shell. Umbilicus cup-shaped, widely opened, last whorl decoiling more rapidly, contained 3.56 times in diameter. Last  $\frac{1}{2}$  whorl missing, hence status of any columellar or palatal dentition unknown. Parietal barriers 2, extending posteriorly about  $\frac{3}{16}$  of a whorl: upper broken off for entire length, only remnants of base present; lower a broad, high, humped lamella with irregularly gradual anterior descension and even, rather steep, posterior descension. Aperture of whole specimen probably inclined about  $15^\circ$  from shell axis. Height of holotype 0.86 mm., diameter 1.88 mm.

**Holotype.**—Marshall Islands: Eniwetok Atoll, Engebi Islet, drill hole K-1B at 820–831 ft. depth (Miocene g). USNM 562091.

**Remarks.**—The spiral apical sculpture, secondary microsculpture of strong spiral cords on the lower whorls, and shape of the remaining parietal barriers immediately place *Vatusila eniwetokensis* in the Charopidae.

Association with recent species is handicapped by the absence of the last half-whorl and resulting loss of any palatal barriers. The combination of 12 apical spiral ribs and a secondary microsculpture of very prominent and widely spaced spiral cords is relatively unusual in the present-day Micronesian charopid fauna. Taxa with approximately these features include only the *Palline notera* complex from Palau and the *Vatusila* radiation from Fiji (Nayau, Lau Group), Tonga (Eua), Niue, and Vaitupu, Ellice Islands. The *Palline notera* complex has simple parietal barriers (probably reduced), whereas *Vatusila* shows a tendency for fusion and reduction of two parietals. The basic shape of the parietals in *V. tongensis* is the same as in *V. eniwetokensis*. The latter could be transformed into the former by partial parietal fusion. *Vatusila tongensis*, *V. kondoi*, and *V. nayauana* share the very strong microsculpture of *V. eniwetokensis*. There are no features allying it to other genera, and I have no hesitation in placing it with *Vatusila*.

***Vatusila tongensis***, new species. Figures 83a–c, 84a–b.

**Diagnosis.**—Shell large, diameter 2.32–2.75 mm. (mean 2.53 mm.), with  $4\frac{1}{4}$ –5 tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending much more rapidly, spire protrusion more than  $\frac{1}{4}$  body whorl width, H/D ratio 0.472–0.650 (mean 0.538). Apical sculpture of 8–12 (mean 10.4) narrow but prominent spiral cords whose interstices are 3–4 times their width. Postnuclear sculpture of high, narrow, rather widely spaced, protractively sinuated radial ribs, 52–72 (mean 61) on the body whorl, whose interstices are 4–6 times their width. Ribs/mm. 6.89–8.71 (mean 7.66). Microsculpture of extremely fine radial riblets, more than 12 between each pair of major ribs, even finer and more crowded spiral riblets, with a secondary microsculpture of prominent spiral cords about twice as large as the microradials, whose interstices are 1–3 times their width. Umbilicus broadly open, U-shaped, regularly decoiling, contained 3.00–4.00 times (mean 3.31) in the diameter, margins rounded. Sutures deep, whorls strongly rounded above, markedly compressed laterally and slightly on basal margin. Aperture subcircular, inclined about  $10^\circ$  from shell axis. Parietal wall with single bifurcated barrier, extending posteriorly more than  $\frac{3}{4}$  of a whorl: upper blade very high and crescentic, gradual posterior descension, rather sharp anterior descension, lower blade shorter posteriorly, elevated medially with same anterior descension found in *Graeffedon*. Both blades mounted on a broad callus that tapers laterally beyond anterior end of bifurcated blade. Columellar wall without barriers. Palatal barriers 2, rather deeply recessed, bulky, extending about  $\frac{1}{4}$  whorl posteriorly: 1st basal in position, slightly to strongly bifurcated, occasionally split into two parts, inner a broad, high, crescentic, rounded, knoblike protuberance usually connected by a callus to a much lower, cordlike blade; 2nd on outer palatal wall, slightly supraparapheral and subperipheral to completely subperipheral, about 0.25–0.36 mm. wide, crescentic in outline, with rather gradual anterior descension, sometimes slightly concave on upper surface with threadlike lamellae.

*Vatusila tongensis* is immediately recognizable by its very large, bifurcated parietal and two very broad palatal barriers. All other *Vatusila* have very slender palatals. No other Pacific Island endodontoids match the palatal barriers. *Vatusila vaitupuensis* and *V. niueana* both have a less protruded spire, much more crowded radial ribbing, and much less conspicuous apertural barriers.

**Description.**—Shell large, with  $4\frac{1}{4}$  tightly coiled whorls. Apex and spire very slightly elevated, last whorl descending moderately, H/D ratio 0.519. Embryonic whorls  $1\frac{1}{2}$ , sculpture mainly eroded with only traces of spiral cording remaining in sutures. Postnuclear whorls with sculpture of widely spaced, high, protractively sinuated radial ribs, rounded above, 72 on the body whorl, whose interstices are 3–5 times their width. Microsculpture of very low and faint radial and spiral riblets crossing much more prominent, rather widely spaced secondary spiral cords. Sutures deep, whorls slightly shouldered above, laterally compressed on outer margins. Umbilicus broadly U-shaped, regularly decoiling, contained 3.00 times in the diameter. Color light yellow-white with broad, somewhat vague flammulations that follow lines of growth. Aperture ovate, flattened laterally, inclined about  $5^\circ$  from shell axis. Parietal wall with a large, crescent-shaped bifid barrier, extending about  $\frac{1}{4}$  whorl, structure as in diagnosis. Columellar wall without barriers. Palatal wall with 2 oddly shaped, recessed barriers: lower a moderately high, irregularly shaped knoblike protuberance with much lower recessed ridgelike outer portion; outer a low, very broad, 0.36 mm. wide callus, extending about  $\frac{1}{4}$  of a whorl. All barriers are very minutely serrated on all portions. Height of holotype 1.38 mm., diameter 2.67 mm.

**Holotype.**—Tonga: Eua, hillside on cliffs east of Ohunua, 2 miles inland at 390 ft. elevation. Collected by H. S. Ladd on May 10, 1928. BPBM 87705.

**Range.**—Eua Island, Tonga.

**Paratypes.**—Eua: cliffs east of Ohunua, 2 miles inland at 390 ft. elevation (9 specimens, BPBM 87705, BPBM 87660); on cliff,  $\frac{1}{2}$  mile inland from Vaigana at 760 ft. elevation (9 specimens, BPBM 87632, BPBM 87693–4); main range on east side (Station T-22) at 1,000 ft. elevation (1 specimen, FMNH 152376).

**Remarks.**—The very peculiar barriers of *Vatusila tongensis* immediately identified this species. The bifid parietal probably originated through partial fusion of two separate barriers, a process that seems to have been carried further in the Ellice Island *V. vaitupuensis* and the Fijian *V. kondoi*. The palatal barriers vary considerably, the lower one usually being low and ridgelike with a lateral fanglike barrier, but often assuming the knoblike form of the type. The outer palatal varies from a flattened, even callus as in the type, to a slanted, basal callus with three or four low, threadlike lamellae on top of it, but generally is without distinct ribbing above.

Fragmentary soft parts were available and are described below.

**Description of soft parts.**—Several fragmentary examples were seen, three of which had the penis and epiphallus present. Vas deferens (fig. 84a, VD) reflexing at penioviducal angle, entering expanded head of epiphallus (E). Latter more than  $\frac{3}{4}$  length of penis, entering latter through fan of penial retractor muscle (PR). Penis 0.9–1.0 mm. long, expanded apically, a strong median bulge, tapering gradually to rather long and slender atrium (Y). Interior (fig. 84b) of penis with a circularly bilobed verge and superior epiphallic pore, biscuit-like stimulator very large and with narrow central crack.

(Based on BPBM 87660 and BPBM 87705, fragmentary parts.)

***Vatusila vaitupuensis***, new species. Figure 85a–d.

**Diagnosis.**—*Vatusila vaitupuensis* has 1 parietal and 2 small palatal barriers, a wider umbilicus, and much more numerous and crowded radial ribs than the Tongan *V. tongensis*. *Vatusila niueana* has a narrower umbilicus, only traces of apertural barriers, and many more radial ribs than *V. vaitupuensis*.

**Description.**—Shell large, with over  $4\frac{1}{2}$  relatively tightly coiled whorls. Apex and spire barely protruding above body whorl, last whorl descending slightly more rapidly, spire protrusion about  $\frac{1}{6}$  body whorl width, H/D ratio 0.487. Apical whorls  $1\frac{3}{4}$ , sculpture of 8 relatively broad, prominent spiral cords, whose interstices are about  $2\frac{1}{2}$  times their width. Postnuclear whorls with low, rounded, crowded, protractively sinuated radial ribs, 115 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets, 3–5 between each pair of major ribs and very inconspicuous crowded spiral riblets. No secondary spiral cording. Sutures relatively shallow, whorls slightly shouldered above, almost evenly rounded on outer margins, very slightly compressed laterally above and below periphery. Umbilicus broadly U-shaped, regularly decoiling, contained 2.89 times in the diameter, margins rounded. Color yellowish white with relatively regular, broad, reddish flammulations that parallel lines of growth. Aperture circular, inclined about  $5^\circ$  from the shell axis. Parietal wall with 1 deeply recessed, low, crescentic barrier (fig. 85d), extending less than  $\frac{1}{4}$  of a whorl. Columellar wall without barriers. Palatal barriers 2: lower a short, broad, cordlike ridge near baso-columellar margin; upper slightly supraparapheral, moderately recessed, extending about  $\frac{1}{4}$  whorl, a low, V-shaped ridge. Height of holotype 1.25 mm., diameter 2.57 mm.

**Holotype.**—Ellice Islands: Vaitupu. Collected by L. Isaacs in May, 1941. BPBM 189681.

**Range.**—Vaitupu, Ellice Islands.



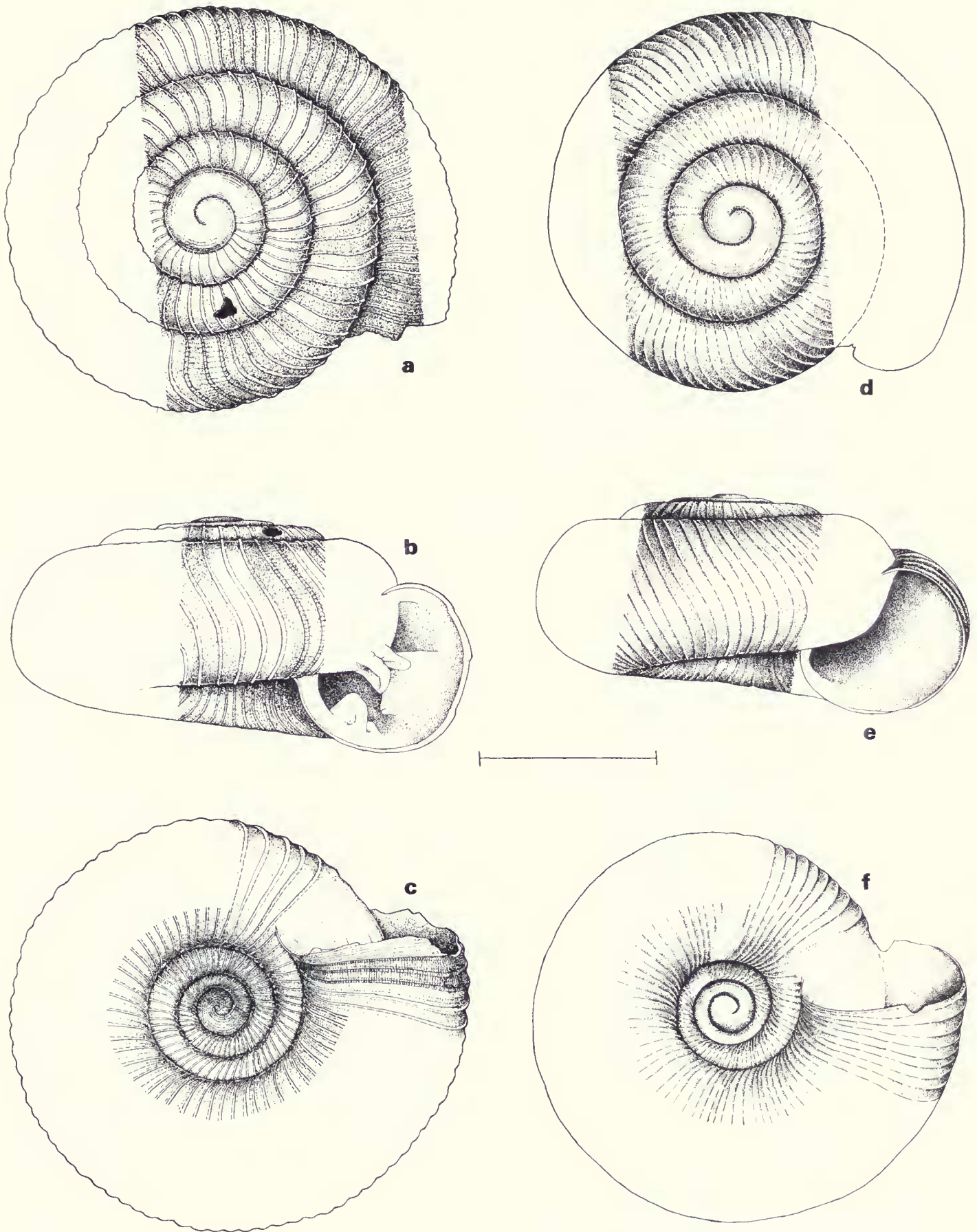


FIG. 83. **a–c**, *Vatusila tongensis*, new species. East of Ohunua, Eua, Tonga. Holotype. BPBM 87705; **d–f**, *Vatusila niueana*, new species. Alofi, Niue. Holotype. BPBM 194517. Scale lines equal 1 mm. (**a–c**, MM; **d–f**, SH).

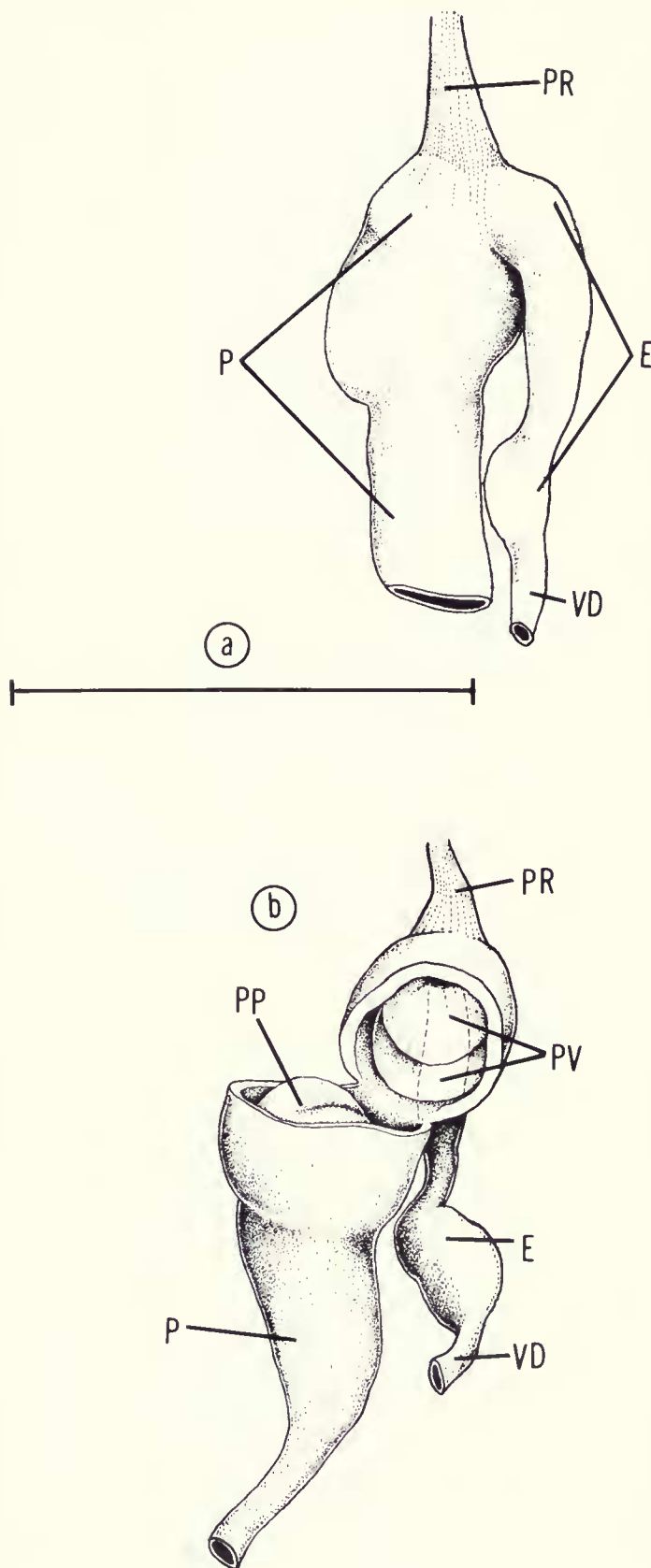


FIG. 84. Partial anatomy of *Vatusila tongensis*, new species. Eua, Tonga. BPBM 87660, BPBM 87705: a, penis and epiphallus; b, vergic papilla and stimulatory pad as seen by opening penis at junction between collar and pad. Scale line equals 1 mm. (MM).

*Paratype*.—Vaitupu (1 specimen, BPBM 189681).

*Remarks*.—Only the adult holotype and a single juvenile specimen are known. The barriers in the latter are relatively more prominent than in the adult, but occupy the same position and have the same shape. The parietal (fig. 85d) closely resembles the upper blade of *V. tongensis* in outline (fig. 83b), but is reduced in size. Similarly, the palatal barriers in *V. vaitupuensis* occupy the same positions as the palatals of *V. tongensis*, but are greatly reduced in prominence.

#### *Vatusila niueana*, new species. Figure 83d–f.

*Diagnosis*.—*Vatusila niueana* has the apertural barriers reduced to barely visible traces. It differs from *V. vaitupuensis* (fig. 85a–d) also in having secondary spiral cording, a much narrower umbilicus, and fewer, less crowded radial ribs. *Vatusila tongensis* (fig. 83a–c) has very large apertural barriers, much more widely spaced radial ribbing, and a distinctly more elevated spire. Differences from geographically adjacent *Sinployea* are discussed below.

*Description*.—Shell large, with  $4\frac{1}{4}$  rather tightly coiled whorls. Apex and spire moderately and almost evenly elevated, last whorl descending much more rapidly, spire protrusion more than  $\frac{1}{6}$  body whorl width, H/D ratio 0.500. Apical whorls  $1\frac{1}{2}$ , sculpture of 10 relatively prominent spiral cords whose interstices are about 3 times their width. Postnuclear whorls with prominent, rounded, rather closely spaced, protractively sinuated radial ribs, 89 on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 11.60. Microsculpture of extremely fine radial riblets, 5–10 between each pair of major ribs, slightly finer spiral riblets, and weak, rather widely spaced secondary spiral cording. Sutures moderately impressed, whorls evenly rounded on outer margins. Umbilicus open, broadly U-shaped, last whorl decoiling slightly more rapidly, contained 3.70 times in the diameter, margins rounded. Color light yellow-white, with a few irregular, reddish flammulations that fade out below periphery. Aperture circular, inclined about  $10^\circ$  from shell axis. Parietal wall with low, broadly angled, slightly submedial swelling, visible from normal side view only as an irregularity in outline (fig. 83e). Columellar, basal, and lower palatal wall with a white callus, narrower and higher at first, becoming broader, lower and more deeply recessed up to periphery of palatal wall. Height of holotype 1.27 mm., diameter 2.44 mm.

*Holotype*.—Niue Island: Alofi Village at 20 m. elevation. Collected on *Pilea microphylla* Liebm. by T. G. Yuncker on February 12, 1940. BPBM 194517.

*Range*.—Niue Island.

*Remarks*.—Even with reasonably careful inspection, *Vatusila niueana* (fig. 83d–f) can be misidentified as a *Sinployea*. The parietal swelling and palatal callus are visible only by tilting and use of oblique lighting into the aperture. I consider it to represent another stage in barrier reduction within the genus *Vatusila*. Although the shell measurements fall just within the range of *Sinployea vicaria* and *S. ellicensis* (table XXIX), in form and whorl contour *V. niueana* is much closer to the other *Vatusila*, the *Sinployea* showing lateral whorl flattening and a higher spire protrusion (*vicaria*, fig. 58b) or much narrower umbilicus (*ellicensis*, fig. 62c). Unfortunately, only the single example, with no soft parts present, was available.



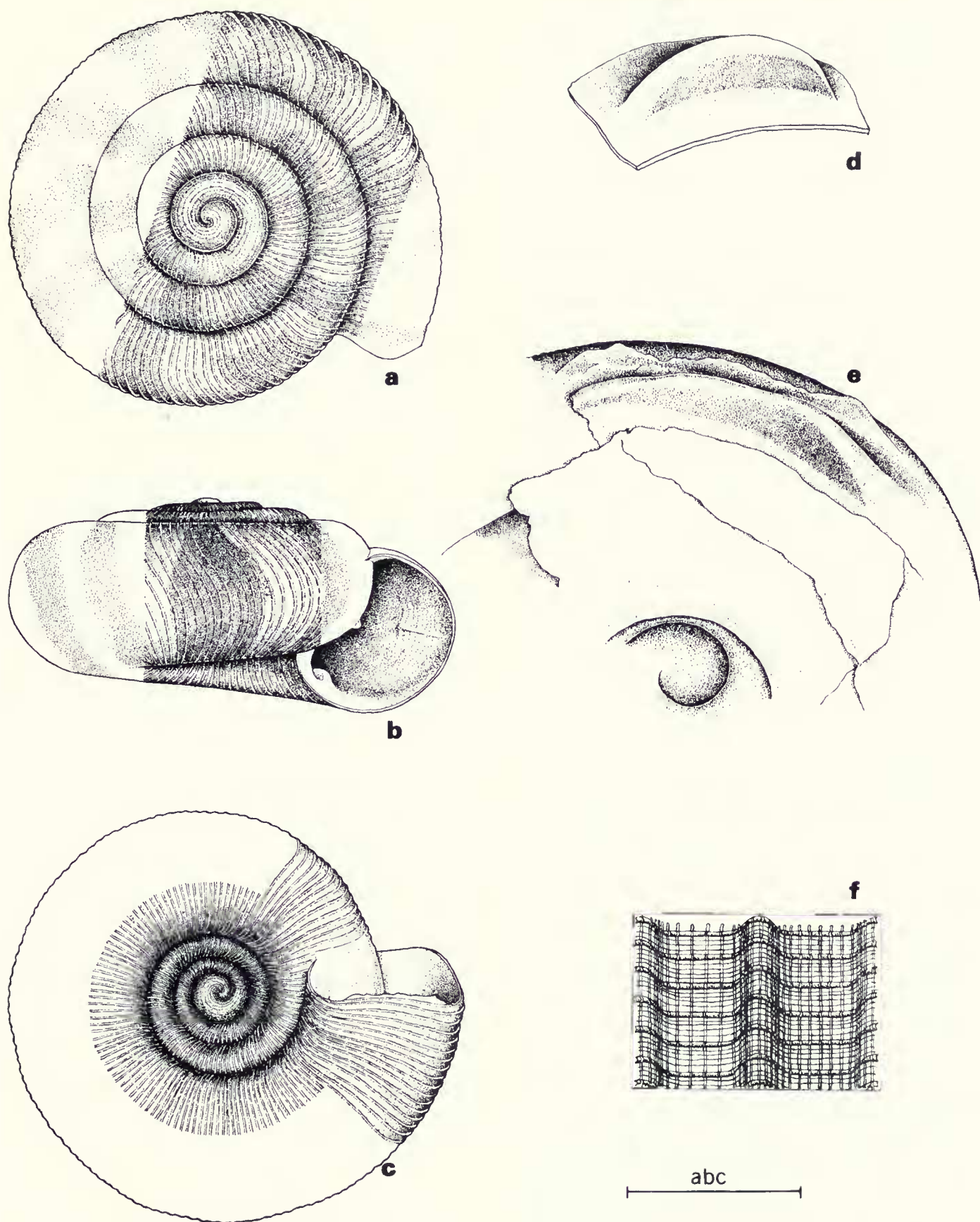


FIG. 85. **a–d**, *Vatusila vaitupuensis*, new species. Vaitupu, Ellice Islands. Holotype. BPBM 189681: **a–c**, entire shell, **d**, parietal barrier; **e–f**, *Vatusila eniwetokensis* (Ladd). Drillhole K-1b at 820–831 ft. depth, Engebi Islet, Eniwetok, Marshall Islands. Holotype. USNM 562091. **e**, lateral view of parietal barriers; **f**, diagram of microsculpture. Scale line equals 1 mm.; **d–f** greatly enlarged. (MM).

Genus *Graeffedon*, new genus

Shell large, with  $4\frac{1}{4}$ – $5\frac{1}{4}$  normally coiled whorls. Apex and spire flat to slightly elevated, body whorl very slightly to moderately descending. Apical sculpture of 11–13 narrow, prominent spiral cords. Postnuclear sculpture of medium to very prominent, protractively sinuated radial ribs, with fine radial and finer microspiral elements, but no spiral cording. Periphery rounded, body whorl slightly flattened laterally above periphery. Umbilicus open, regularly decoiling. Color flammulations zigzagged. Parietal wall with 2 barriers, extending posteriorly about  $\frac{1}{2}$  whorl, upper with rather sharp anterior descension, lower with more gradual anterior descension. Columellar wall with or without a low threadlike ridge parallel to plane of coiling, recessed or reaching lip margin. Palatal barriers 4 to 7, short, high, almost reaching lip edge, sometimes with weak accessory traces. Pallial region with rectal kidney lobe much larger and longer than pericardial, a distinct intrusion of mantle gland tissue onto pallial roof. Apical genitalia apparently without unusual features. Epiphallus with simple entrance of vas deferens, followed by 2 high pilasters. Penis with an apical muscle ring, and 3 large pilasters, 1 probably acting as a vergic papilla. Lower female tract with simple pore opening from free oviduct into common chamber of vagina and spermatheca, which is lined with high, longitudinal pilasters.

*Type species.*—*Endodonta graeffei* Mousson, 1869.

The most similar shells are those of *Semperdon*, particularly examples of *S. heptapychius* (Quadras & Möllendorff, 1894) (fig. 99a–c, e) and *S. rotanus* (fig. 99d). Their penial anatomy (fig. 100b, d–g, k) is so totally different from that of *Graeffedon* (fig. 87b–c) that the shell similarities clearly are convergent. Even optical microscopic examination of the apertural barriers shows that there are differences in microarmature between the two genera, and the SEM photos of *Graeffedon* (fig. 7a–c) and *Semperdon xyleborus* (fig. 8a–e) demonstrate that they are formed quite differently (see pp. 19–20).

*Graeffedon* stands quite isolated from other Pacific Island Charopinae in terms of anatomical structure. The simple vas deferens-epiphallus juncture, very large penial pilasters, and strong pilasters within the vaginal-spermathecal chamber are quite different from those found in the typical Charopinae. It is quite possible that eventual subfamily separation of *Graeffedon* will be required, but until many more extralimital taxa have been studied, retention of *Graeffedon* within a broadly defined Charopinae is preferred.

The only genus with which I can at present relate *Graeffedon* in terms of anatomy is *Helenoconcha* Pilsbry, 1892, from St. Helena in the South Atlantic. The only dissected species, *Helenoconcha relictata* Solem (1977c, figs. 184a–b, 185a–d), agrees in pallial structure (except for lacking the mantle gland intrusion) and has exactly the same type of penial structure. The two taxa differ only in details of pilaster position and size, but the penis complex of *Helenoconcha* is remarkably similar to *Graeffedon*. At present the internal structures of the terminal genitalia in the South African endodontoid taxa, *Trachycystis* Pilsbry, 1893, and *Afrodonta* Melville & Ponsonby, 1908, are unknown (see Solem, 1970c), but the external genital features of *Trachycystis* illustrated by Watson (1934, pls. 20–21) are compatible with at least the latter genus being a member of this complex.

It is thus premature to attempt formal designation of a subfamily unit for *Graeffedon*.

Specimens of *Graeffedon* are rare in collections and in the field. The three species differ in size, sculpture, and details of the palatal barriers (see Diagnoses). Because of their allopatric distribution, no structural key is presented. Their known distributions are:

*Graeffedon graeffei*—Upolu, Samoa

*G. savaiiensis*—Savai'i, Samoa

*G. pricei*—Tongatapu, Tonga.

***Graeffedon graeffei* (Mousson, 1869). Figures 7a–c, 86a–c, 87a–d.**

*Endodonta graeffei* Mousson, 1869, J. de Conchyl. 17, pp. 332–333, pl. 14, fig. 3—Upolu, Samoa.

*Pityx graeffei* (Mousson), Pease, 1872, Proc. Zool. Soc. London, 1871, p. 474; Garrett, 1887, Proc. Acad. Nat. Sci. Philadelphia, 1887, pp. 130–131.

*Helix (Endodonta) graeffei* (Mousson), Pfeiffer, 1876, Monog. helic. viv., 7, p. 258; Tryon, 1887, Man. Conchol., (2) 3, p. 65, pl. 12, fig. 31.

*Endodonta (Thaumatodon) graeffei* (Mousson), Pilsbry, 1893, Man. Conchol., (2) 9, p. 27.

*Diagnosis.*—Shell very large, diameter 4.61–5.92 mm. (mean 5.23 mm.), with  $4\frac{1}{4}$ – $5\frac{1}{4}$  rather tightly coiled whorls. Apex and early spire flat or barely protruding, lower spire descending slightly, body whorl much more rapidly, spire protrusion about  $\frac{1}{11}$  body whorl width, H/D ratio 0.472–0.560 (mean 0.525). Apical sculpture of 11–13 (mean 12.0) narrow but prominent spiral cords whose interstices are 4–5 times their width. Postnuclear sculpture of high, prominent, V-shaped to U-shaped, crowded, slightly protractively sinuated radial ribs, 92–121 (mean 105.0) on the body whorl, whose interstices are 2–3 times their width. Ribs/mm. 6.27–6.51 (mean 6.39). Microsculpture of proportionately fine radial riblets, 5–8 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. No secondary spiral cording. Umbilicus moderately open, V-shaped, regularly decoiling, contained 3.53–4.19 times (mean 3.94) in the diameter, margins rounded. Whorls distinctly flattened laterally above periphery and on basal margin, aperture inclined about 15° from shell axis. Parietal barriers 2, extending posteriorly slightly more than  $\frac{1}{2}$  whorl; upper very high and broadly expanded above posteriorly, this portion deflected downward, then gradually descending and narrowing to anterior quarter, then abruptly descending on anterior 8th; lower broadly expanded, serrated, and crescentic on posterior half, narrowing above and with even descension anteriorly. Columellar wall with (40%) or without (60%) a low, broadly rounded, high, threadlike ridge, lying parallel to plane of coiling and reaching lip margin. Palatal barriers 5, high and prominent, reaching almost to lip margin; lower 4 progressively higher, longer, more slender, changing from abrupt to more gradual anterior descension, all crescentic, with height about  $\frac{2}{3}$  length, extending posteriorly less than  $\frac{1}{2}$  whorl, with 1st at basal-columellar margin; 4th subperipheral; lower 2 have anterior edge turned inward just before reaching lip; upper supraperipheral, greatly reduced in height, a bladelikey barrier with equally gradual anterior and posterior descension, longer than 4th, and slightly recessed within aperture.

*Graeffedon graeffei* is much larger than the Savai'i Island *G. savaiiensis* or the Tongan *G. pricei* (table XLIII). The former has a much wider umbilicus, seven palatal barriers, finer sculpture, an elevated apex, and more rounded whorls; the latter has fewer and more prominent radial ribs, only four palatal barriers, a flat apex, and is smaller in size.



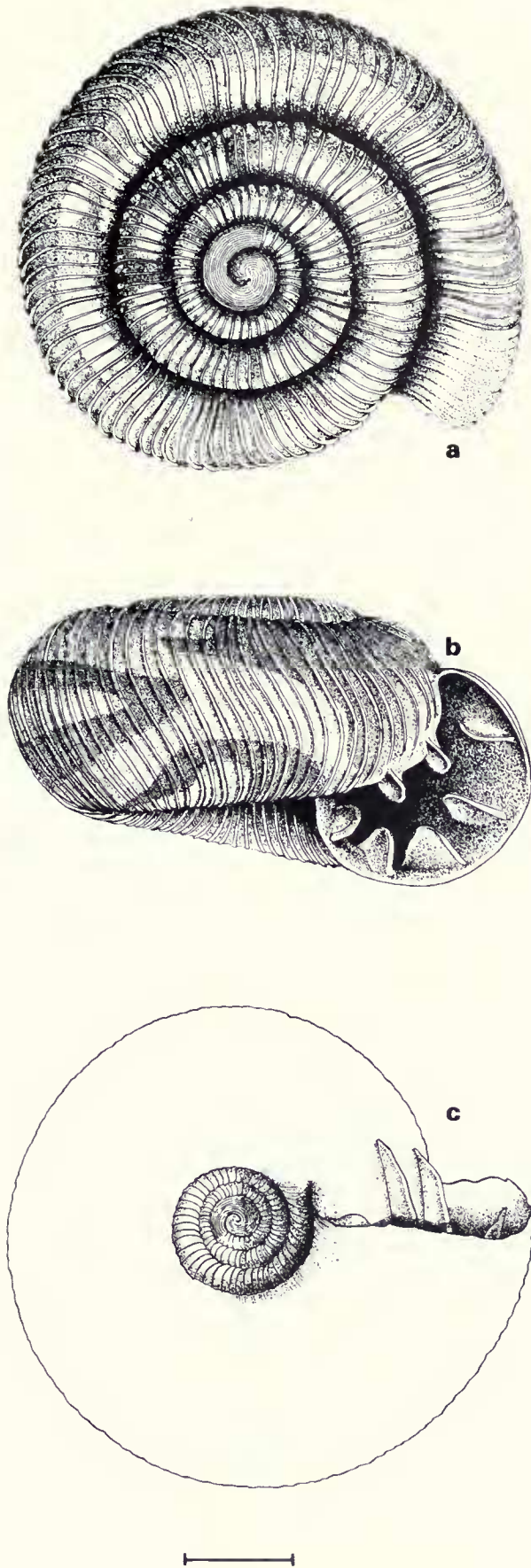


FIG. 86. a-c, *Graeffedon graeffei* (Mousson). Upolu, Samoa. Lectotype. Zoologisches Institut der Universität Zurich. Scale line equals 1 mm. (SG).

*Description*.—Shell very large, with slightly more than 4½ moderately tightly coiled whorls. Apex and early spire flat, later whorls descending a little, body whorl more rapidly, H/D ratio 0.527. Apical whorls 1½, sculpture of 12 narrow cords. Postnuclear sculpture of high, prominent, crowded, protractively sinuated radial ribs, 98 on the body whorl, whose interstices are 2–3 times their width. Microsculpture a lattice of fine, relatively crowded and numerous radial riblets, 5–8 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Sutures deeply impressed, whorls strongly rounded above, somewhat flattened laterally above periphery and slightly on basal margin. Umbilicus moderately open, V-shaped, regularly decoiling, contained 3.93 times in the diameter. Color light yellowish white with very prominent zigzag reddish brown flammulations. Aperture subovate, flattened laterally above periphery, inclined about 15° from the shell axis. Parietal barriers 2, extending a little more than ¼ whorl: upper high, bladelike, slightly expanded above posteriorly with relatively sharp anterior descension; lower more crescentic, more broadly expanded above with comparatively gradual anterior descension. Columellar wall without barriers. Palatal barriers 5, reaching lip margin, short and crescentic: lower at baso-columellar margin, sharply descending to lip edge; 2nd, 3rd, and 4th crescentic, very high, slightly expanded above, 2nd reaching lip margin with very sharp anterior descension, 3rd slightly recessed with more gradual descension, 4th a little more recessed with much more gradual anterior descension; upper a longer, lower, ridgelike lamella, narrow above with very gradual posterior rise and anterior descension. All barriers minutely pustulose or serrated above. Basal and columellar portion of lip with a low, broad, white callus. Height of holotype 2.60 mm., diameter 4.94 mm.

*Holotype*.—Samoa: Upolu. Collected by E. Graeffe. Zoologisches Museum der Universität, Zurich.

*Range*.—Probably the uplands of Upolu, Western Samoa.

*Material*.—Upolu (4 specimens, Zurich, Brussels, FMNH 116976, FMNH 147544): summit of Mt. Solaua (Station 39) under ground debris in heavy forest at 2,000 ft. elevation (1 specimen, FMNH 153420).

*Remarks*.—Besides the type in the Mousson collection, two specimens were found in museums identified as *Sinployea complementaria* (Mousson, 1865). A single example was collected under rotting wood in 1965 together with 18 specimens of *S. complementaria*. In size and general appearance (figs. 56a–f, 86a–c) the two species are very similar, with the elevated spire and narrower umbilicus of *S. complementaria* (fig. 56a–f) not being obvious during field examination. Externally the animal of *Graeffedon graeffei* differs in having the body without any grayish markings on the neck and sides of the foot. The absence of apertural barriers in *S. complementaria* and their presence in *G. graeffei* immediately separate the two species.

In order to dissect the one specimen, partial destruction of the shell was necessary. The soft parts broke during extraction, but reasonably full study of the anatomy was possible. The significant differences have been discussed previously (p. 29).

*Description of soft parts*.—Foot and tail completely retracted into shell. Sole and pedal grooves typical, no caudal horn or middorsal groove developed. Slime network conspicuous. Body color yellow-white, no trace of darker markings.

Mantle collar (MC) partly shredded during extraction because of large barriers, a prominent glandular extension (MG) onto pallial roof. Anus (A) opening slightly in front of external ureteric pore (KX), vague grooves leading through pneumostomal opening.

TABLE XLIII. - RANGE OF VARIATION IN GRAEFFEDON.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER		
<u>graeffei</u> (Mousson)	5	105(92-121)	6.39(6.27-6.51)	2.75(2.37-3.26)	5.23(4.61-5.92)		
<u>savaiensis</u>	1	88	8.43	1.61	3.32		
<u>pricei</u>	1	68	6.52	1.61	3.32		
	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS		
<u>graeff.</u>	0.525(0.472-0.560)	5-(4 3/4-5 1/4)	1.36(1.15-1.48)	3.94(3.53-4.19)	12.0(11-13)		
<u>savai.</u>	0.485	4 1/4	1.02	3.26	11		
<u>pricei</u>	0.485	4 1/8-	0.92	3.61	WORN		
	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW	PR	C	P	
<u>graeff.</u>	0.17(0.10-0.20)	1.83(1.68-2.04)	0.092(0.058-0.118)	2	0-1	5	
<u>savai.</u>	0.15	1.05	0.141	2	1	7	
<u>pricei</u>	FLAT	1.13	-----	2	0	4+2	

Pallial region (fig. 87a) extending about 5.5 mm., distance from anus to anterior tip of kidney 1.65 mm. Lung roof clear, without granulations. Kidney (K) bilobed, pericardial lobe less than half length of rectal lobe, very narrow, rectal lobe crossing hindgut into parietal wall, length 3.85 mm. Ureter (KD) with short primary arm jammed between lobes of kidney with no lung roof visible, secondary ureter widening along hindgut. Heart (H) angled to hindgut, slightly more than half length of pericardial kidney lobe. Principal pulmonary vein (HV) unbranched and inconspicuous, reaching to edge of mantle collar extension. Hindgut (HG) extending well past pallial cavity apex before leaving parietal-palatal margin.

Ovotestis (fig. 87d, G) a single clump of large, long acini, palmately clavate, lying parallel to whorl sides above stomach apex. Hermaphroditic duct (GD) long, expanded evenly for most of length, abruptly narrowing before reflexing to enter base of globular talon. Albumen gland completely destroyed by parasites in dissected example. Talon (not shown) large, globular, with very narrow neck to carrefour. Prostate (fig. 87b, DG) of large acini opening into groove in inner uterine wall, variously folded. Uterus (UT) bipartite, upper chamber thin-walled and narrow, lower grossly expanded and thick-walled.

Vas deferens (VD) tapering and with glandular walls to penioviducal angle, narrow and muscular after passing through muscle threads, entering epiphallus without special structures. Epiphallus (E) larger than penis, curved and twisted, internally (fig. 87c) with one very high and rounded and a second lower and hemispherical pilaster that taper into epiphallic pore. Penial retractor (PR) a broad muscle band arising from diaphragm and inserting in a narrow line onto head of penis along middle zone of apical penial pilaster. Penis (P) about 1.48 mm. long, sharply constricted subapically, then tapering. Internally (fig. 87c) with a dome-shaped pilaster and epiphallic pore (EP) on one side of center occupying area above constriction, below with a huge spade-shaped pilaster tapering to atrium. Lateral to this a "hoe"-shaped pilaster tapering to a broad glandular ridge and a high, longitudinal pilaster tapering into glandular area. Atrium (Y) short, without marked features.

Free oviduct (UV) muscular, short, with glandular walls. Spermatheca (S) with expanded head next to albumen gland, slender shaft bound to prostate-uterus, expanded basal portion with 2 large

and several smaller tapered pilasters (fig. 87c). Vagina (V) with many narrow pilasters, externally with numerous muscle strands holding it to the body wall.

Esophagus distended, typical in position, stomach occupying  $\frac{2}{3}$  of a whorl. Intestinal looping without unusual features. Digestive glands mostly replaced by parasites above stomach apex, partly in region of esophagus-stomach junction. Salivary glands united above esophagus, right gland greatly reduced in size.

(Based on 1 adult, FMNH 153420.)

### Graeffedon savaiensis, new species. Figure 88a-c.

*Diagnosis.*—*Graeffedon savaiensis* differs from the Upolu *G. graeffei* (Mousson, 1869) in its slightly and regularly elevated apex, possession of 7 palatal barriers, wider umbilicus, and much smaller size. The Tongan *G. pricei* (fig. 88d-f) has a flat apex and spire, much coarser radial ribbing, lower and shorter parietals, and only 4 major palatals, although essentially identical in size and proportions.

*Description.*—Shell slightly larger than average, with  $4\frac{1}{4}$  normally coiled whorls. Apex and spire slightly and evenly elevated, last whorl not descending more rapidly, spire protrusion about  $\frac{1}{4}$  body whorl width, H/D ratio 0.485. Apical whorls  $1\frac{1}{2}$ , sculpture of 11 thin, relatively high, spiral cords. Postnuclear whorls with thin, lamellate, protractively sinuated radial ribs, 88 on the body whorl, whose interstices are 2-4 times their width. Ribs/mm. 8.43. Microsculpture of fine radial riblets, 3-6 between each pair of major ribs, with much finer and more crowded spiral riblets. Sutures moderately impressed, whorls strongly rounded above suture, slightly flattened laterally and on basal margin with evenly rounded periphery. Umbilicus widely open, V-shaped, last whorl decoiling more rapidly, contained 3.26 times in the diameter. Color light yellow-white with irregular reddish brown flammulations becoming darker on body whorl. Aperture ovate, slightly flattened laterally above periphery, inclined about  $10^\circ$  from shell axis. Parietal barriers 2, extending posteriorly  $\frac{1}{4}$  whorl: upper very high and crescentic posteriorly, serrated and expanded above, flattening out anteriorly, then descending rather sharply on anterior 8th; 2nd a much lower, bladelike lamella, broadly expanded above and slightly elevated posteriorly, with gradual descension over anterior half. Columellar wall with single,



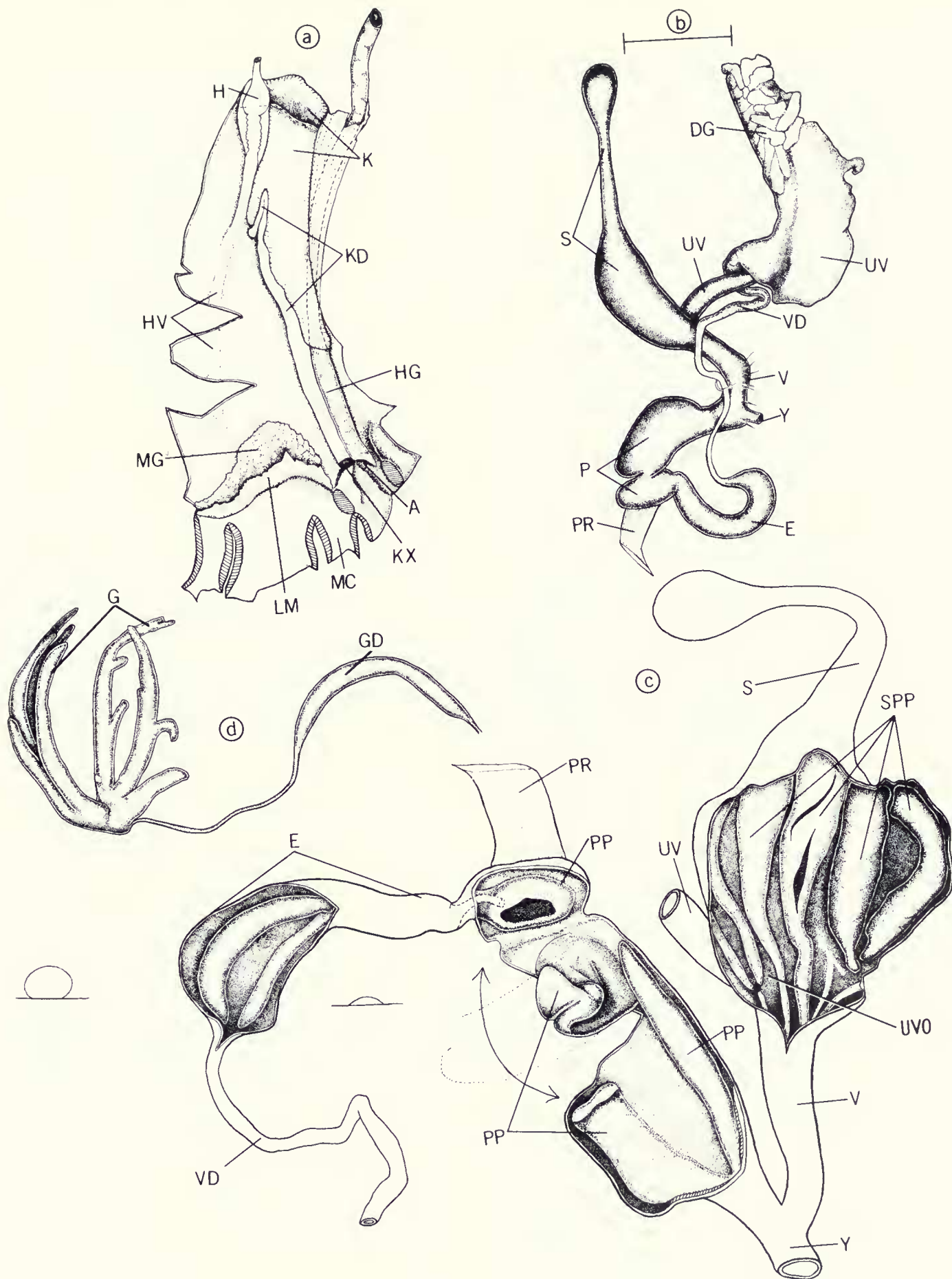


FIG. 87. Anatomy of the Samoan *Graeffedon graeffei* (Mousson). Station 39, Mt. Solaua, Upolu, Samoa. FMNH 153420: a, pallial region; b, genitalia; c, interior of penis, epiphallus, spermathecal base; d, ovotestis and hermaphroditic duct. Scale lines equal 1 mm. (SH).

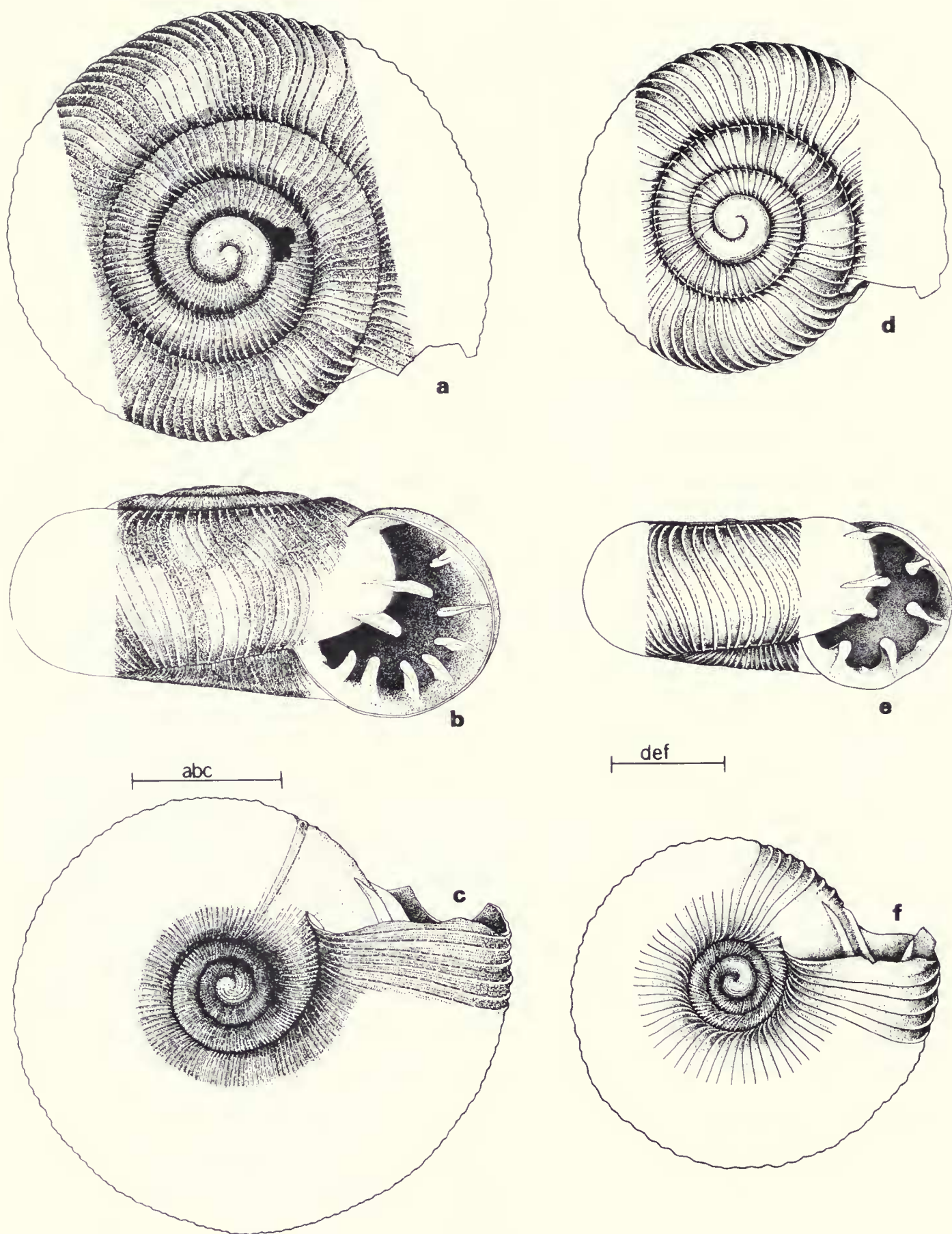


FIG. 88. a-c, *Graeffedon savaiensis*, new species. Mataulano Lake, Savai'i, Samoa. Holotype. BPBM 95738; d-f, *Graeffedon pricei*, new species. Manima Id., Tongatapu, Tonga. Holotype. FMNH 152399. Scale lines equal 1 mm. (a-c, MM; d-f, SH).



low, threadlike ridge, lying parallel to plane of coiling, reaching top of columellar callus. Palatal barriers 7, short, high, reaching lip margin for early ones, then later barriers slightly recessed: lower at baso-columellar margin, hemispherical, very high, with abrupt anterior descension, curving back inward at lower anterior margin; 3rd, 4th, and 5th progressively lower, longer, less expanded above, changing to more gradual anterior descension with 5th crescentic, all subperipheral; 6th equal in height to 5th, slightly supra-peripheral, with more gradual anterior descension; 7th high, bladelike, much lower than 6th, slightly concave above, moderately expanded, with gradual anterior descension, injured anteriorly, slightly recessed within aperture. All palatals weakly serrated on upper edge and sides. Height of holotype 1.61 mm., diameter 3.32 mm.

*Holotype*.—Samoa: Savai'i, near Mataulano Lake. Collected in leaf mould on a hillside by E. Christopher-son on October 2–3, 1929. BPBM 95758.

*Range*.—Interior of Savai'i, Western Samoa.

*Material*.—Known only from the holotype.

*Remarks*.—The elevation of Mt. Mataulano is 2,952 ft., but I have no data as to the elevation of the lake at which this species was collected. The single shell is probably subadult, but the distinctness from *G. graeffei* is based on the former having smaller nuclear whorls, a flat apex and early spire, wider and higher major radial ribs, and a noticeably narrower umbilicus. Shape of the parietal barriers is identical, but in *G. savaiiensis* they are shorter and proportionately higher. Besides the increased number of palatals, in *G. savaiiensis* they are shorter and hemispherical in outline, rather than being crescentic. The columellar in *G. savaiiensis* is lower and more deeply recessed.

Despite particular effort by Mr. Price, no specimens were collected on Savai'i in 1965.

### *Graeffedon pricei*, new species. Figure 88d–f.

*Diagnosis*.—*Graeffedon pricei* differs from the Savai'i *G. savaiiensis* in its flat apex and spire, heavier and less crowded ribbing, smaller parietals, and presence of only 4 palatals. *Graeffedon graeffei* from Upolu is much larger, has the body whorl descending much more rapidly, and has proportionately much larger apertural barriers.

*Description*.—Shell slightly larger than average, with a little less than  $4\frac{1}{2}$  rather tightly coiled whorls. Apex and spire flat, body whorl descending slightly, H/D ratio 0.485. Apical whorls  $1\frac{3}{4}$ , sculpture eroded except for traces of narrow spiral cords in sutures and umbilicus. Postnuclear whorls with very prominent, wide, protractively sinuated radial ribs, 68 on the body whorl, whose interstices usually are 2–4 times their width. Microsculpture mostly obscured, visible on spots as consisting of very fine radial riblets, 6–12 between each pair of major ribs, crossed by slightly finer and more crowded spiral riblets. Sutures impressed, whorls strongly rounded above and on periphery, slightly compressed laterally above and below periphery. Color leached from shell, with faint traces of reddish flammulations visible above periphery. Umbilicus open, broadly V-shaped, regularly decoiling, contained 3.61 times in the diameter. Aperture circular, slightly compressed laterally above and below rounded periphery, inclined about  $10^\circ$  from shell axis. Parietal barriers 2, relatively low, extending posteriorly  $\frac{1}{4}$  whorl: upper elevated on posterior quarter, expanded and serrated above, gradually descending to anterior threadlike quarter; 2nd equal in height, slightly more expanded above on elevated posterior quarter, rather sharply descending to midpoint, anterior half a high threadlike ridge. Columellar wall without barriers. Palatal barriers 4, high, bulbously expanded above, short, reaching lip edge, with two threadlike accessory traces: lower at baso-columellar margin, hemispherical, anterior descension abrupt, margin deflected inward just before

lip; 2nd slightly higher, equally expanded above, with sharp anterior descension, but no inward deflection; 3rd equal in height, slightly subperipheral, with more gradual anterior descension; 4th supra-peripheral, reduced in height, a bladelike lamella strongly expanded above, slightly recessed, with gradual anterior descension. Accessory traces low and threadlike, located midway between 1st and 2nd, 2nd and 3rd palatals, slightly recessed, shorter than major palatals. Height of holotype 1.61 mm., diameter 3.32 mm.

*Holotype*.—Tonga: Tongatapu, Manima Island, 4 miles northeast (Station T-4) of Nuku'alofa in second growth on a coral atoll. Collected by Laurie Price on January 26, 1966. FMNH 152399.

*Range*.—Probably Tongatapu and its satellite islands, Tonga.

*Material*.—Only the holotype is known.

*Remarks*.—*Graeffedon pricei* is identical in height and diameter to the single known example of *G. savaiiensis*, but readily separable by the characters cited in the diagnosis. Its aperture is more evenly rounded, and the ribbing difference is particularly obvious. The position of the major palatals and two accessory palatal traces in *G. pricei* does not correspond to the position of the palatals in *G. savaiiensis* or *G. graeffei*.

Collections on Tongatapu were made during a severe drought. No living endodontids were collected and comparatively little live material in other groups. Great pleasure is taken in naming this species after Mr. Laurie Price of Kaitaia, New Zealand, in grateful recognition of his collecting activities for Field Museum of Natural History.

### Subfamily TRUKCHAROPINAE, new subfamily

Formal description of this subfamily has been given on p. 70.

Several genera confined to the Palau and Caroline Islands show major anatomical modifications. In sharp contrast to the Charopinae and Semperdoninae, there is no indication of differentiation into a vas deferens and an epiphallus. The vas starts as a thin-walled transparent tube that rapidly changes into the typically muscular shiny state seen in almost all endodontoid species. There may be slight diameter changes at the penioviducal angle, but usually the tube retains a constant diameter until entering the penis. Except in *Jokajdon*, these genera all agree in having the vas deferens tranverse the penis head, then passing through the penial retractor muscle fan before entering the penis. In both the Charopinae and Semperdoninae, there is a prominent epiphallus developed, with a complicated valvular entrance present in many Charopinae (figs. 29i–j, 57e).

Although the Palau and Caroline Island genera grouped as the Trukcharopinae share this basic pattern of vas deferens-penis junction, there is much greater diversity in internal penial structure and moderate divergence in other genital features. The degree of genital difference between these genera is much greater than that which is seen in the Pacific Island

Charopinae and Semperdoninae, and involves both addition and elimination of structures. Shell structure is diverse, with an array of large and small, tightly and loosely coiled, heavily sculptured and with reduced sculpture, with and without barriers, elevated spires to deeply depressed apices all represented. Pallial organs show variation, but not to an extreme extent. Only 11 species are involved, but their range of diversity exceeds that in the other subfamilies.

At this time I prefer not to speculate on the mutual affinities of these genera. Except for *Jokajdon* and *Palikirus*, which could be monophyletic, the differences are large enough that I am somewhat dubious of local derivation. Until enough Australian and New Zealand charopids have been dissected to establish the pattern of variation within that complex, the possibility that the Micronesian genera represent relicts from an early faunal migration from Southeast Asia through New Guinea to Australia, New Zealand, and New Caledonia cannot be excluded. Such an early migration would be prior to the spread of the helicarionid taxa presently dominant in the Indonesian-New Guinea Archipelago. Although the Semperdoninae and generalized Charopinae appear monophyletic with reasonably clear patterns of change, the Trukcharopinae share the lack of an epiphallus and enfolding of the vas deferens within the penial retractor muscle but represent a great variety of other experiments.

Major items of anatomical differences are summarized in the following paragraphs. *Roimontis tolotomensis*, *Palline biakensis*, and *Palikirus ponapicus* have not been dissected and thus are excluded from the following discussion.

Variations in the pallial cavity involve length, degree of kidney overlap onto the parietal wall, relative length of the pericardial and rectal kidney lobes, and shape of the kidney. Pallial cavity length is about three-quarters of a whorl in *Jokajdon* (fig. 93a); one-half whorl in *Palikirus*, *Palline*, *Trukcharopa*, and *Kubaryiellus*; and one-quarter whorl in *Russatus* (fig. 90a). The square shape and equal kidney lobe length in *Russatus* is correlated with the whorl count reduction and coiling change. The other genera have elongated kidneys with the lobes of unequal length. In *Jokajdon* (fig. 93a), *Palline* (fig. 93e, g) and *Kubaryiellus* (fig. 90e) the rectal lobe is twice the length of the pericardial; in *Palikirus* and *Trukcharopa* the rectal lobe is 20%–30% longer than the pericardial. There is not a direct correlation between lobe length and parietal wall overlap, because there is moderate overlap in *Palline* and *Palikirus*, strong overlap in *Jokajdon*, slight overlap in *Trukcharopa*, and no overlap in *Kubaryiellus* and *Russatus*. In *Jokajdon* and *Palline* the pericardial kidney arm is greatly reduced in width as well as length, but in *Palikirus*, with moderate kidney overlap, the pericardial arm is not reduced in size. I could not correlate the degree of overlap or differences in lobe length with shell features such as coiling pattern or body whorl width. Possibly the size factor is

critical because the three small genera, *Jokajdon*, *Palline*, and *Palikirus*, have marked kidney overlap onto the parietal wall, whereas the larger genera do not. More data are needed.

Previous extraction of the soft parts in many species meant that the apical genitalia could not be studied. Often the apical part of the visceral hump breaks off when the animal is pulled out. It remains in the shell and subsequently dries up. Thus only partial data are available on a dichotomy into species having one or two alveolar clumps in the ovotestis. No size correlation exists, since the very small *Jokajdon* and quite large *Kubaryiellus* have a single clump, whereas the small *Palline* and medium-sized *Trukcharopa* have two distinct clumps, one lying completely apicad of the other, with both touching the palatal surface of the whorl. I could not examine the ovotestis of *Palikirus* or *Russatus*. In *Jokajdon* the ovotestis alveoli were fewer in number and proportionately much larger and longer than in the other genera. Sufficiently accurate measurements for comparison of midvisceral genitalia proportions were not obtained. I saw no qualitative or obvious proportional differences in this area.

Distinctions are present in proportions and relative development of the free oviduct, spermatheca, and vagina. Normally the basal portion of the spermathecal shaft is greatly expanded in the Charopidae, with the interior having various complicated glandular or muscular pilasters and ridges (fig. 87c). *Jokajdon* is radically different in lacking any expansion of the lower spermathecal shaft (fig. 93b). It also is the only Micronesian genus in which the vagina is distinctly longer than the free oviduct. *Russatus* (fig. 90c) has a short vagina and a short free oviduct with the base of the spermathecal shaft globosely and suddenly expanded. These features correlate with the reduced whorl count and shortened pallial cavity, because a zonal compaction of the midvisceral genitalia typically accompanies such an alteration in coiling pattern. The other four genera have rather long free oviducts. In *Palikirus* the vagina is quite short; in *Kubaryiellus* (fig. 90f), *Trukcharopa* (fig. 90i), and *Palline* (fig. 93f, h) the vagina is slightly shorter than the free oviduct. Spermathecal shaft expansion is essentially the same in *Palikirus* and *Kubaryiellus*, with the gradual tapered expansion occurring over a distance equal to the free oviduct length. In *Trukcharopa* there is a relatively sharp expansion that occurs over little more than half of the free oviduct length, whereas in *Palline* there is very gradual expansion that starts about at the mid-uterine level, well above the free oviduct origin. The functional significance of these changes is unknown.

Fundamental differences exist in the penial complex. Most of these are concerned with the functioning surfaces of the penis, but even just external shape and proportions show major alterations. *Palline* (fig. 93f, h), *Trukcharopa* (fig. 90i), and *Palikirus* agree in having an ovately to globosely expanded penial head following



a much shorter, narrow tube (almost equal to head length in *Trukcharopa*). *Russatus* is basically the same, except that the expanded head is clearly triangular in shape (fig. 90b). *Kubaryiellus* (fig. 90f) has a very long, club-shaped penis with the shaft tapering gradually to the atrium. *Jokajdon* (fig. 93b) has the penis tapered apically and basally from a median expansion. Penial size is best expressed in relation to shell diameter because *Russatus* is  $2\frac{1}{4}$  times the diameter of *Jokajdon*. Three genera, *Russatus*, *Palikirus*, and *Jokajdon*, have a long penial retractor muscle, and the ratio of total penis length to shell diameter is between 0.15 and 0.30. *Palline* and *Kubaryiellus* have short penial retractor muscles, and the ratio is between 0.45 and 0.60. *Trukcharopa* has a short penial retractor and total penis length almost equals the shell diameter. Because origin of the penial retractor muscle normally lies near the apex of the pallial cavity, increasing relative penis length shortens the penial retractor. Unlike many Endodontidae, no Pacific Island Charopidae have the penial retractor muscle detached from the diaphragm and joined to the free retractor system.

Internally, *Palline* has a tubular verge that apically may function as an epiphallic chamber; *Kubaryiellus*, a trilobed vergic papilla (fig. 90h); *Russatus* (fig. 90d), a simple pore with a lateral, rather long caecum on the inner wall of the penis head; *Jokajdon*, *Palikirus*, and *Trukcharopa* (fig. 90j), a simple pore with no major apical structures in the penis. Some form of muscular "pocket" pilaster is found in *Jokajdon*, *Palikirus*, and *Trukcharopa*, with the pilaster globular in *Palikirus*, of the *Sinployea*-type in *Jokajdon*, and greatly changed in *Trukcharopa*. Weak apical longitudinal pilasters are found in *Jokajdon* and *Palikirus*, strong submedial longitudinal pilasters in *Kubaryiellus*. *Russatus* has weak, circular glandular pilasters, whereas *Palline* has a lateral pocket with concentric glandular pilasters and a large, median thick circular or partly circular pilaster. *Jokajdon* is unique in having a separate free retractor muscle attached to the penioviducal angle.

Of the above changes, the verge and circular pilasters in *Palline*, internal caecum in *Russatus*, penioviducal angle muscle in *Jokajdon*, and major longitudinal pilasters in *Kubaryiellus* represent entirely new structures. Opening of the vas deferens into the penis through a simple pore in *Russatus*, *Palikirus*, *Jokajdon*, and *Trukcharopa* represents a loss of structure when compared with the Charopinae. Other structures could be relatively simple modifications from the *Sinployea* pattern, but the items detailed above represent loss or gain of entire structures.

Factors of shell variation are discussed in greater detail elsewhere (pp. 8–23). Here it is necessary to note only a few points. It is the smallest shells, *Jokajdon* and *Palline*, that have the tightest coiling pattern (figs. 92a, d; 94a) and greatest development of apertural barriers (fig. 92b, e). The largest shells, *Kubaryiellus* and *Russatus*, have the loosest form of

coiling (fig. 89a–f) and totally lack apertural barriers. Only *Palline* and *Palikirus* show the normal charopid shell coloration of simple yellow-horn or with traces of darker flammulations. The remaining genera have the shell reddish (*Jokajdon*, *Trukcharopa*), reddish brown (*Kubaryiellus*, *Roimontis*), or deep reddish purple-brown (*Russatus*). Only *Palline* (fig. 94b) has a moderately elevated spire, most of the others have it normally flat or slightly elevated, whereas in *Kubaryiellus* (fig. 89b) the apex is distinctly depressed, and in *Roimontis* (fig. 91a–b) it is very depressed. Umbilical width shows only moderate variation, with slight narrowing in *Palline* (fig. 94c) and great narrowing in *Russatus* (fig. 89f). Sculpture is greatly reduced in *Russatus*, greatly enlarged in *Palikirus* (fig. 91d–f). Interpretation of these variations is rendered difficult by the high concentration of species on Ponape. *Palline notera* is found on Koror, Peleliu, and Babelthuap in the Palau Islands; *Palline biakensis*, on Biak Island, West Irian; and *Trukcharopa* is restricted to the Truk Group and Lukunor in the Central Carolines. The remaining eight species are restricted to Ponape. We have no exact locality for *Palikirus ponapicus* (Möllerndorff, 1900), but the other seven species were taken at one or more stations by the B. P. Bishop Museum Micronesian Expedition in early 1936. Several species live together, because three to five species were collected at four stations (table XLIV). No data exist concerning any ecological separation of the species. The genital differences, except between the two species of *Jokajdon*, cannot be ascribed to a simple character displacement phenomenon. The size of the penis itself is so different between sympatric forms, and both deletion and addition of structures are involved.

Ponape offers considerable opportunities for investigation of isolating mechanisms in land snails because the multitude of sharply differentiated charopids there is equivalent to the remarkable radiation of trochomorphid genera and species, *Kondoa*, *Hogolua*, and *Brazieria* in the Truk Group (Baker, 1941, pp. 272–280), and *Trochomorpha* itself on Ponape (Baker, 1941, pp. 290–296). Rapa shows an even greater radiation of Endodontidae (Solem, 1976b, pp. 490–492), but these taxa show far less dramatic changes in genital structures, a much greater amount of local geographic speciation, and probably are extinct.

#### Genus *Trukcharopa*, new genus

Shell of average size, with about 4% normally coiled whorls. Apex and spire flat to slightly elevated, body whorl descending slightly. Apical sculpture of about 10 prominent spiral cords. Post-nuclear sculpture narrow, crowded, protractively sinuated radial ribs, averaging about 18/mm. on body whorl. Microsculpture of fine radial riblets, finer spiral, and prominent secondary spiral cords. Umbilicus widely open, margins rounded. Whorls only slightly compressed laterally above and below rounded periphery, aperture inclined about 20° from shell axis. No apertural barriers developed. Pallial region extending  $\frac{1}{2}$  whorl apically, with rectal kidney arm 20%–30% longer than pericardial. Ovary with 2 clumps of alveoli, 1 above other, hermaphroditic duct partly convoluted. Penial retractor muscle relatively short, enfolding vas deferens before inserting

TABLE XLIV. - SYMPATRY OF CHAROPIDAE  
ON PONAPE, CAROLINE ISLANDS.

Station 91	
<u>Palikirus</u>	<u>cosmetus</u>
<u>Kubaryiellus</u>	<u>kubaryi</u>
<u>Jokajdon</u>	<u>tumidulus</u>
<u>Jokajdon</u>	<u>callizonus</u>
Station 92	
<u>Roimontis</u>	<u>tolotomensis</u>
<u>Russatus</u>	<u>nigrescens</u>
<u>Kubaryiellus</u>	<u>kubaryi</u>
<u>Jokajdon</u>	<u>tumidulus</u>
<u>Jokajdon</u>	<u>callizonus</u>
Station 93	
<u>Roimontis</u>	<u>tolotomensis</u>
<u>Russatus</u>	<u>nigrescens</u>
<u>Jokajdon</u>	<u>tumidulus</u>
<u>Jokajdon</u>	<u>callizonus</u>
Station 139	
<u>Palikirus</u>	<u>cosmetus</u>
<u>Kubaryiellus</u>	<u>kubaryi</u>
<u>Jokajdon</u>	<u>tumidulus</u>

on penis head. Penis long, head greatly expanded, internally with a huge medial stimulator, no vergic papilla, weak papillose glandular walls in lower tube. Spermatheca with basal part of shaft greatly expanded, vagina relatively long.

*Type species.*—*Trukcharopa trukana*, new species.

Both *Kubaryiellus* and *Trukcharopa* have much longer penes (fig. 90f, i) than any of the other Micronesian genera that lack an epiphallus, but the structures of the penes are very different. *Trukcharopa* has the head grossly expanded, lacks a vergic papilla, and has a huge median muscular stimulatory pad on one wall of the expanded chamber (fig. 90i–j). Serial sections of the penial region will be required before the exact structure of this stimulatory pad can be determined, but the essential differences from the other Micronesian genera are obvious.

*Trukcharopa* is nearest in shell structure to the Polynesian-Melanesian genus *Sinployea*. Anatomic-

cally the two differ in *Sinployea* having a prominent epiphallus that is about half the penis in length, the penis has a distinct vergic papilla, and the typical stimulatory pad occupies the median part of the penis. *Sinployea kusaieana* is the only named Micronesian species in that genus. Conchological comparisons with *Trukcharopa trukana* (tables XXVII, XLV) show that they are virtually identical in mean diameter, umbilical width, D/U ratio, and body whorl width. *Sinployea kusaieana* (fig. 63a–c) is a light reddish yellow and has an average of 91 major radial ribs, 10.3–13.1 ribs/mm. on the body whorl, with five to 10 microradial riblets between each pair of major ribs. In contrast, *Trukcharopa trukana* (fig. 63d–f) is dark reddish brown in color and has an average of 150 major radial ribs, 14.1–20.8 ribs/mm. on the body whorl, with only two to four microradials between each pair of major ribs. I could find no conchological features in *Trukcharopa* that would differentiate it generically from *Sinployea*. Both pallial region and male genital structures (fig. 90i–j) place *T. trukana* as being more closely related to the Micronesian genera than to *Sinployea*.

In choosing *Trukcharopa* as a name for this genus, I am reflecting both its great similarity to the traditionally named "*Charopa*" (= *Sinployea*) of Polynesia and its geographic location.

***Trukcharopa trukana*, new species.** Figures 63d–f, 90i–j.

*Diagnosis.*—Shell smaller than average, diameter 2.50–3.08 mm. (mean 2.66 mm.), with 4¼–4¾ rather tightly coiled whorls. Apex and early spire normally flat, sometimes slightly protruding, rarely moderately elevated, body whorl usually descending slightly more rapidly, spire protrusion generally much less than ¼ body whorl width, occasionally moderately elevated, H/D ratio 0.371–0.513 (mean 0.450). Apical sculpture of 8–12 (mean 9.68) prominent spiral cords, whose interstices are 2–3 times their width. Postnuclear sculpture of low, narrow, crowded, slightly protractively sinuated radial ribs, 112–197 (mean 150.1) on the body whorl, whose interstices usually are 1½–2 times their width. Ribs/mm. 14.1–20.8 (mean 17.7). Microsculpture of very fine, rather widely spaced radial riblets, 2–4 between each pair of major ribs, much finer and more crowded spiral riblets, with a secondary sculpture of spiral cords that are more prominent than the microradial riblets and whose interstices are about 3–4 times their width. Umbilicus broadly open, V- to U-shaped, regularly decoiling, contained 3.07–4.00 times (mean 3.43) in the diameter, margins evenly rounded. Sutures deep, whorls strongly rounded above, slightly compressed laterally above periphery and on basal margin, with evenly rounded outer and columellar margins. Aperture subovate, compressed laterally above periphery and on basal margin, inclined about 20° from shell axis. No apertural barriers, but a weak to moderate callus extending from columellar region up to periphery in some individuals.

*Trukcharopa trukana* is much smaller, has much more crowded radial ribbing, more apical cords, and lacks the depressed spire of *Kubaryiellus kubaryi* (Möllendorff) (fig. 89a–c). *Russatus nigrescens* (Möllendorff) has fewer whorls, a looser coiling pattern, and is much larger in size (fig. 89d–f). Differences from the Kusaie Island *Sinployea kusaieana* (fig. 63a–c) are covered in the generic discussion above.

*Description.*—Shell rather small, with slightly more than 4¼ relatively tightly coiled whorls. Apex and spire flat, last whorl barely



TABLE XLV. - RANGE OF VARIATION IN MICRONESIAN CHAROPINAE, I.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER
<u>Sinployea</u> <u>kusaieana</u>	61	91.1(84-103)	11.25(10.27-13.12)	1.32(1.19-1.49)	2.60(2.52-2.75)
<u>Trukcharopa</u> <u>trukana</u>	405	150.1(112-197)	17.7(14.07-20.84)	1.19(0.99-1.42)	2.66(2.50-3.08)
<u>Kubaryiellus</u> <u>kubaryi</u>	52	112.2(99-132)	9.54(8.39-11.70)	1.86(1.59-2.25)	3.74(3.36-4.60)
<u>Russatus</u> <u>nigrescens</u>	30	R E D U C E D		2.20(1.91-2.66)	4.81(4.34-5.53)
<u>Roimontis</u> <u>tolotomensis</u>	2	57.5(57-58)	6.64(6.27-7.01)	1.46(1.39-1.52)	2.78(2.65-2.91)
<u>Palikirus</u> <u>cosmetus</u>	8	18.9(17-21)	2.51(2.29-2.71)	1.23(1.12-1.38)	2.40(2.17-2.58)
<u>ponapicus</u>	1	46	6.74	0.99	2.17

	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO
<u>kusei.</u>	0.506(0.462-0.542)	3 7/8+(3 3/4-4 1/8)	0.74(0.69-0.79)	3.51(3.21-3.67)
<u>truks.</u>	0.450(0.371-0.513)	4 3/8-(4 1/8-4 3/4)	0.77(0.63-0.95)	3.43(3.07-4.00)
<u>kubar.</u>	0.494(0.453-0.540)	4 1/8-(3 7/8-4 1/2)	1.01(0.83-1.32)	3.70(3.36-4.24)
<u>nigres.</u>	0.455(0.418-0.482)	3 1/8+(3 1/8-3 1/2)	0.53(0.30-0.69)	10.6(6.30-16.5)
<u>tolot.</u>	0.524(0.523-0.525)	4	0.71(0.69-0.72)	3.91(3.81-4.00)
<u>cosme.</u>	0.510(0.487-0.542)	3 3/4+(3 5/8-4)	0.70(0.63-0.82)	3.44(3.14-3.67)
<u>ponap.</u>	0.454	3 3/8	0.54	4.00

	APICAL CORDS	SPIRE ELEVATION	BODY WHORL WIDTH	SP/BWW	PR
<u>kusei.</u>	9.2(8-10)	0.119(0.099-0.164)	0.72(0.79-0.86)	0.150(0.125-0.208)	0
<u>truks.</u>	9.68(8-12)	0.08(FLAT-0.23)	0.80(0.72-0.87)	0.092(FLAT-0.264)	0
<u>kubar.</u>	7.62(6-9)	DEPRESSED	1.41(1.32-1.58)	-----	0
<u>nigres.</u>	REDUCED	SLIGHTLY DEPRESSED TO FLAT	1.29(1.18-1.41)	-----	0
<u>tolot.</u>	6.50(6-7)	DEEPLY DEPRESSED	1.13(1.07-1.18)	-----	2
<u>cosme.</u>	11.80(10-13)	0.17(0.15-0.20)	0.76(0.72-0.79)	0.228(0.205-0.250)	1
<u>ponap.</u>	9	N O T A V A I L A B L E			0

descending, H/D ratio 0.430. Embryonic whorls  $1\frac{1}{2}$ , sculpture of 8 prominent, rather closely spaced spiral cords. Postnuclear whorls with prominent, narrow, crowded, protractively sinuated radial ribs, 133 on the body whorl, whose interstices are 2-3 times their width. Microsculpture of very fine radial riblets and even finer spiral riblets, crossed by prominent, widely spaced secondary spiral cords that become wider and more numerous on the body whorl. Sutures deep, whorls evenly rounded above, markedly flattened laterally above periphery and on basal margin. Umbilicus broadly U-shaped, regularly decoiling, contained 3.59 times in the diameter. Color reddish brown. Aperture ovate, flattened basally and laterally above periphery, inclined about  $5^\circ$  from the shell axis. Height of holotype 1.12 mm., diameter 2.60 mm.

*Holotype*.—Caroline Islands, Truk, Tol Islet, Station A5, on dead leaves, 1,200 m. inland, near top of Mt. Urupot. Collected by K. Atoda on February 17, 1940. BPBM 189318.

*Range*.—Truk Group and Lukunor, Caroline Islands.

*Paratypes*.—Truk: Moen Islet: Nebokos (Station 16), from shore to  $\frac{1}{4}$  mile inland at 4-5 ft. elevation (4 specimens, BPBM 153701-2); west side of Mt. Teroken (Station 18), 1 mile inland at 900 ft. elevation (2 specimens, BPBM 153792); Saboku Village (Station A4), under dead leaves (105 specimens, BPBM 189263). Fefan Islet: Urunna village (Station A3), near shore on dead leaves (26 specimens, BPBM 189179). Dublon Islet: Mt. Tolowan (Station 9), in native forest at 850 ft. elevation (53 specimens, BPBM 153385-92); Mt. Tolowan (Stations 1, 8, 11) at 300-800 ft. elevation (3 specimens, BPBM 153072, BPBM 153451); Meseran Village (Station 12), northeast part of island, 1-100 ft. inland at 1-12 ft. elevation (5 specimens, BPBM 153506). Param Islet: 200 ft. back of beach (Station 37) at 3 ft. elevation (1 specimen, BPBM 155749). Tarik Islet (Stations 38, A2; 3 specimens, BPBM 153911,

BPBM 155762, BPBM 189423). Tol Islet: Mt. Urupot (Stations 28, 29, 30, A5, A7), halfway up to summit, 1,000–1,200 m. inland, 700–1,422 ft. elevation (109 specimens, BPBM 155550–4, BPBM 153879–82, BPBM 155477–8, BPBM 155508, BPBM 189318, BPBM 189343); Urifei (Station A6), on dead leaves (9 specimens, BPBM 189334); Iruku, Tsukuran village (Station A1), 100 m. inland on dead leaves (13 specimens, BPBM 189406); southwest slope of Mt. Urupot, 1 mile inland above spring, 1,000–2,000 ft. elevation (35 specimens, BPBM 210864, BPBM 210890–2, BPBM 210921). Oneap Islet (9 specimens, ANSP 191994). Nama Islet (2 specimens, ANSP 191995). Ta Islet (25 specimens, ANSP 192000). Lukunor (3 specimens, AMS C.7561).

*Remarks.*—Probably *Trukcharopa trukana* occurs on most of the islets in the Truk Group. Numerous specimens were collected on Moen, Fefan, Dublon, and Tol Islets. Only three living specimens were found on Tarik and one dead shell from Param Islet. Several sets from the Thaanum collection were obtained on exchange by the ANSP. These sets undoubtedly contain selected fragments of larger field samples, and the slight size and shape differences shown by these (table XLVI) probably reflect sample bias rather than any morphologic changes. The cited names of Oneap, Nama, and Ta Islets are taken from the ANSP labels. I was not able to identify the position of Oneap and Ta.

Ignoring the differences in the ANSP samples, there is only minor shape variation present. Comparing the specimens from Tol and Moen (table XLVI), the differences in height ( $t = 3.6106$  with 21 degrees of freedom), H/D ratio ( $t = 2.8764$ ), and D/U ratio ( $t = 2.3826$ ) reach statistical significance. The shells from Tol all have a flat spire and hence a lower H/D ratio, lower height, and slightly wider umbilicus than those from other islets where some individuals have a slightly elevated spire. I attach no systematic importance to this variation. Specimens from Tol have much fewer and more widely spaced major radial ribs than do those from Moen or Oneap. Shells from Ta (ANSP 192000) are intermediate. Possibly there is an ecological correlation involved, but I have no data concerning this situation.

Where large numbers of specimens were taken, the percentage of adults is very low. Probably the greater number of adults in small samples reflects collecting bias, at least in part, but the pattern of juvenile predominance is clear. Data for six stations are presented in Table XLVII. The collecting dates range from December to May and from 1935 to 1940. Two different collectors were involved. No pattern of seasonality is suggested.

Four specimens from Lukunor (AMS) are referred here with some hesitation. They appear to be slightly subadult, and if allowance is made for this, they fit within the range of variation for *Trukcharopa trukana*. Pending receipt of more adequate material, I classify these shells as this species.

Several penes were opened, but I am not certain of the details shown in Figure 90j concerning the exact stimulatory pad structure. All specimens had many bits and strands of material inside, and determination of details was not possible from gross dissections. Time did not permit preparation of serial sections. The difference between the *Sinployea*-type stimulator and that of *Trukcharopa trukana*, the former a pocket behind and above a U-shaped muscle band, with the latter a longitudinally oriented structure, combined with the presence of an epiphallus in *Sinployea* and its absence in *Trukcharopa* are sufficient to distinguish the two genera without difficulty.

*Description of soft parts.*—Foot and tail about  $\frac{2}{3}$  shell diameter in length, not tapering posteriorly, broadly rounded behind, truncated anteriorly. Sole undivided, pedal grooves high on foot, pedal much deeper, grooves uniting over tail with slight depressions, but no caudal horn or middorsal groove developed. Slime network without unusual features. Gonopore in normal position. Body color light yellow-white, without darker markings.

Mantle collar without glandular extension onto pallial roof. Anus and external ureteric pore with same position. Pallial region extending  $\frac{1}{2}$  whorl apically. Lung roof clear. Kidney about 1.2–1.3 mm. long, rectal arm longer than pericardial arm, which is about 1 mm. from anterior end to base. Ureter typical, section between kidney arms tightly compacted, overlapped by kidney. Heart about half length of pericardial kidney arm. Principal pulmonary vein unbranched. Hindgut typical.

Ovotestis (fig. 90i, G) with two clumps of palmately clavate alveoli, located in half whorl above stomach apex, lying parallel to whorl margins and occupying most of whorl space, slightly iridescent in tone. Hermaphroditic duct partly convoluted, tapering apically, constricted just before entering base of talon head. Albumen gland (GG) short and compact, acini relatively small. Talon (GT) with globular head, very short shaft to carrefour region. Prostate (DG) of comparatively few and large acini opening into groove on inner side of uterus. Uterus (UT) bipartite, lower chamber much larger and with thick, glandular walls.

Vas deferens (VD) slender for entire length, passing through penial retractor muscle while crossing head of penis, then inserting laterally on penis head. Penial retractor (PR) arising from diaphragm, slightly shorter than expanded penis head, inserting on head of penis after enfolding vas deferens. Penis (P) with expanded globular head, about 1.3 mm. long, followed by a narrow tube that is equal in length to penis head or slightly shorter, internally (fig. 90j) expanded head with an almost hemispherical stimulator (PP) lying partly unattached against one wall of penis, no vergic papilla, vas entering through a simple pore. Internal structure quite complex and should be studied using serial sections. Atrium (Y) narrow and rather long.

Free oviduct (UV) larger than penis head, wider above. Spermatheca (S) with elongately oval head, very slender shaft, strongly expanded laterally. Vagina (V) usually longer than illustrated, a simple tube. Free muscle and digestive system without unusual features.

(Based on BPBM 189263, 2 whole individuals 2.43 mm. in diameter with  $4\frac{1}{4}$  whorls and 2.57 mm. in diameter with  $4\frac{1}{4}+$  whorls, plus several extracted fragments.)

### Genus *Kubaryiellus*, new genus

Shell large, with about  $4\frac{1}{4}$  rather loosely coiled whorls. Apex and spire depressed, body whorl not descending. Apical sculpture of 6–9 very prominent spiral cords. Postnuclear whorls with narrow, prominent, protractively sinuated radial ribs, averaging less than 10/mm. on the body whorl. Microsculpture of prominent radial riblets, finer spirals, and prominent secondary spiral cords. Umbilicus moderately open, V-shaped, margins rounded. Whorls flattened lat-



TABLE XLVI. - LOCAL VARIATION IN TRUKCHAROPA.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>trukana</u>						
Oneap ANSP 191994	6	168.8±7.46 (143-197)	19.0±0.550 (16.98-20.50)	1.27±0.032 (1.19-1.39)	2.85±0.055 (2.70-3.08)	0.452±0.0034 (0.442-0.460)
Nama ANSP 191995	2	157	17.98	1.13±0.017 (1.12-1.15)	2.70±0.083 (2.62-2.78)	0.421±0.0065 (0.414-0.427)
Ta ANSP 192000	11	139.3±3.14 (124-156)	17.3±0.359 (15.07-19.24)	1.21±0.019 (1.08-1.27)	2.57±0.023 (2.45-2.68)	0.469±0.0078 (0.420-0.506)
Dublon Sta. 9 BPBM 153385,-506	7	-----	-----	1.16±0.017 (1.09-1.23)	2.64±0.029 (2.52-2.75)	0.440±0.0091 (0.398-0.468)
Tol Sta.A5,A6,A7,30 BPBM 155550, BPBM 189318,-34,-43	12	122.5 (112-133)	15.2 (14.09-16.28)	1.14±0.024 (0.99-1.29)	2.64±0.036 (2.52-2.95)	0.433±0.0090 (0.371-0.487)
Moen Sta.A4, 16 BPBM 153701, BPBM 189263	11	164.7 (147-183)	18.5 (16.54-20.80)	1.26±0.023 (1.16-1.42)	2.71±0.041 (2.55-2.91)	0.466±0.0069 (0.432-0.513)
Fefan Sta.A3 BPBM 189179	5	-----	-----	1.23±0.026 (1.19-1.32)	2.72±0.056 (2.58-2.88)	0.454±0.0058 (0.437-0.471)
Lukunor AMS C7561	4	114.8±2.78 (107-120)	16.6±0.859 (15.01-19.02)	1.06±0.032 (0.97-1.12)	2.20±0.067 (2.01-2.30)	0.480±0.0052 (0.471-0.493)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
Oneap	4 1/2-(4 1/4-4 3/4)	0.86 (0.76-0.95)	3.29±0.074 (3.07-3.59)	10.67±0.335 (10-12)
Nama	4 1/4	0.81±0.050 (0.76-0.86)	3.36±0.105 (3.25-3.46)	10.0
Ta	4 1/4-(4 1/8-4 3/8)	0.75±0.015 (0.63-0.82)	3.42±0.066 (3.18-3.97)	10.36±0.244 (9-12)
Dublon	4 1/4+(4 1/8-4 1/2)	0.74±0.023 (0.63-0.79)	3.57±0.087 (3.29-4.00)	9.86±0.261 (9-11)
Tol	4 3/8-(4 1/4-4 5/8)	0.79±0.019 (0.72-0.95)	3.33±0.052 (3.07-3.63)	8.73±0.305 (8-11)
Moen	4 3/8-(4 1/8-4 5/8)	0.78±0.017 (0.69-0.86)	3.48±0.033 (3.27-3.67)	9.20±0.250 (8-10)
Fefan	4 1/2-(4 1/4-4 1/2)	0.76±0.028 (0.69-0.82)	3.57±0.058 (3.40-3.71)	9.75±0.480 (9-11)
Lukun.	4-(3 3/4-4 1/8)	0.58±0.028 (0.53-0.66)	3.79±0.140 (3.40-4.06)	-----

erally above and below rounded periphery, aperture inclined about 15° from shell axis. No apertural barriers. Pallial cavity with rectal kidney arm about twice length of pericardial, otherwise without unusual features. Ovotestis with one clump of alveoli, hermaphroditic duct tightly convoluted. Vas deferens passing through penial retractor muscle before entering laterally on penis head. Penis very long, club-shaped, tapering, internally with a trilobed vergic papilla followed by 2 long, stimulatory pilasters on a papillose glandular wall. A thin muscle sheath surrounds penis. Spermatheca typical, vagina somewhat longer than typical.

*Type species.*—*Charopa kubaryi* Möllendorff, 1900.

*Roimontis tolotomensis* (fig. 91a-c) is most similar in shell features, but differs in having spiral grooves rather than spiral cords, two parietal barriers, fewer and more widely spaced radial ribs, a much more depressed spire, and it is smaller in size. *Russatus nigrescens* (fig. 89d-f) has a flat spire, much looser coiling, a very narrow umbilicus, reduced radial sculpture, greatly altered pallial region, and quite different genital structures. *Trukcharopa trukana* (fig. 63d-f) has a flat to slightly elevated spire, much more numerous and crowded radial ribs on a much smaller shell, a tighter coiling pattern, finer apical sculpture, and the penis not only lacks a muscle sheath but has much different internal structure.

*Kubaryiellus* (fig. 89a-c) has a modified shell. Its depressed apex and spire with relatively loose coiling are unusual in the Pacific Island Charopidae, but the

TABLE XLVII. - AGE DISTRIBUTION IN TRUKCHAROPA TRUKANA.

ISLET	STATION	DATE OF COLLECTION	NUMBER OF ADULTS	NUMBER OF SHELLS COLLECTED	% OF ADULTS
Moen	A3	May 1, 1940	5	26	19.2%
	A4	May 24, 1940	9	105	8.6%
Dublon	9	Dec. 20, 1935	7	53	13.2%
Tol	A5	Feb. 17, 1940	5	24	20.8%
	A6	May 9, 1940	2	9	22.2%
	30	Jan. 4, 1936	3	47	6.4%

systematically important features are the greatly altered penial complex. This agrees with most other Micronesian genera in having the vas deferens pass through the penial retractor muscle, but the distinct penial muscle sheath, trilobed vergic papilla, and two enlarged longitudinal pilasters (fig. 90g) represent major departures from the structural pattern seen in the other genera. The penial length of 1.95–2.20 mm. is much greater than that seen in the other Micronesian genera that lack an epiphallus. The vergic papilla could be derived from the type seen in *Sinployea irregularis* (fig. 67d) by elongation and size increase, but the absence of an epiphallus, development of a distinct sheath, and the peculiar pilasters are very different from the *Sinployea* pattern.

*Kubaryiellus* is named in honor of I. Kubary, pioneer collector of land mollusks in New Guinea and the Caroline Islands for Otto von Möllendorff.

**Kubaryiellus kubaryi** (Möllendorff, 1900). Figures 89a–c, 90e–h.

*Charopa kubaryi* Möllendorff, 1900, J. Malacol., 7 (5), p. 110—Ponape, Caroline Islands.

**Diagnosis.**—Shell large, diameter 3.36–4.60 mm. (mean 3.74 mm.) with  $3\frac{3}{4}$ – $4\frac{1}{2}$  normally coiled whorls. Apex and spire distinctly depressed below level of body whorl, last portion of body whorl barely descending, H/D ratio 0.453–0.540 (mean 0.494). Apical sculpture of 6–9 (mean 7.62) prominent spiral cords, whose interstices are about twice their width. Postnuclear sculpture of prominent, narrow, lamellar, crowded, protractively sinuated radial ribs, 99–132 (mean 112.2) on the body whorl, whose interstices are 3–6 times their width. Ribs/mm. 8.39–11.70 (mean 9.54). Microsculpture of prominent radial riblets, 3–6 between each pair of major ribs, much finer and more crowded spiral riblets, with rather widely spaced secondary spiral cords equal in size to or slightly larger than microradial riblets. Umbilicus broadly V-shaped, regularly and rapidly decoiling, contained 3.36–4.24 times (mean 3.70) in the diameter, margins evenly and gently rounded. Sutures deep, whorls strongly rounded above and on baso-columellar margin, strongly compressed laterally above rounded periphery with slightly compressed lower palatal margin. Aperture subovate, strongly compressed laterally above periphery, inclined about  $15^\circ$  from shell axis. No callus or apertural barriers developed.

In having a distinctly depressed apex and marked lateral flattening of the body whorl, *Kubaryiellus kubaryi* is immediately separated from other Micronesian or Polynesian species. *Roimontis tolotomensis* (fig. 91a–c) has the apex much more deeply depressed, two weak parietals, and is much smaller.

**Description.**—Shell large, with  $4\frac{1}{4}$  overlapping whorls. Apex and early spire distinctly sunken, markedly overlapped by coiling of later whorls, last portion of body whorl descending only slightly below top of penultimate, H/D ratio 0.458. Apical whorls  $1\frac{1}{2}$ , sculpture of 7 widely spaced, relatively narrow spiral cords. Postnuclear whorls with somewhat irregular, narrow, moderately protractively sinuated radial ribs, relatively widely spaced on spire, becoming crowded on last whorl, about 132 on body whorl, whose interstices are 1–3 times their width. Microsculpture of fine, irregularly spaced radial riblets crossed by finer, slightly more crowded spiral riblets with a secondary sculpture of moderately prominent, widely spaced spiral cords. Sutures moderately impressed, whorls strongly rounded above, strongly flattened laterally above obtusely rounded periphery with evenly rounded basal margin. Umbilicus broadly V-shaped, regularly decoiling, contained 3.43 times in the diameter, with margins slightly shouldered. Color light reddish

yellow-brown above, apex yellow-horn, and a narrow yellowish white spiral band situated  $\frac{1}{3}$  of the way between suture and periphery of the whorl. Periostracal ends of ribs in sutures and in umbilicus dark chocolate brown. Aperture ovate, moderately flattened laterally above periphery, inclined about  $10^\circ$  from the shell axis. Height of lectotype 1.81 mm., diameter 3.95 mm.

**Lectotype.**—Caroline Islands: Ponape. Collected by Kubary. SMF 165352.

**Range.**—Ponape, Caroline Islands.

**Paratypes.**—BPBM 86245, SMF 165353.

**Material.**—Ponape (1 specimen, BPBM 87528): back of Naupilo (Station 133) (4 specimens, BPBM 157564–5); Paishapel Hill, Metalanim (Station 113), at 650–700 ft. elevation (14 specimens, BPBM 157211–6); west side Tolomaim Mt. (Station 91) at 1,000–1,500 ft. elevation (3 specimens, BPBM 154002–3); Metalanim to Mipit (Station 118), 450 ft. inland at 300–900 ft. elevation (6 specimens, BPBM 154157–60); Mt. Kuporujō (Station 121) at 500–900 ft. elevation (1 specimen, BPBM 154338); southwest side of To-reairuka Mt. (Station 127) at 250–750 ft. elevation (6 specimens, BPBM 154451–3); one quarter to halfway up Mt. Tolotom (Station 92) at 800 ft. elevation (1 specimen, BPBM 156677); north slope Mt. Nanalaut (Stations 129, 130) at 1,600–2,500 ft. elevation (2 specimens, BPBM 157443); Mt. Nanalaut (Station 129A) at 1,900 ft. elevation to top (1 specimen, BPBM 154523); Palikir, Jokaj (Station 139 = 138), at 600–900 ft. elevation (3 specimens, BPBM 157797); Palikir, Mt. Tamantamansakir (Station 140) at 1,000–1,250 ft. elevation (6 specimens, BPBM 157864).

**Remarks.**—Relatively few individuals of *Kubaryiellus kubaryi* were taken at any single station, but it is widely distributed on Ponape. From stations where individuals were measured, 39 shells were collected, of which 20 (51.3%) were adult. This is by far the highest percentage of adult specimens for any Caroline species of which more than 10 examples were collected.

Spire depression is marked, but much less than in *Roimontis tolotomensis*, and there is no noticeable reduction in umbilical depth.

Dissection of several penes showed variation in the length and exact form of the vergic papilla. The figured example (fig. 90g, PV) had the shortest seen, the lower lobes are sometimes extended for almost half the penis length in a U-shaped form, the upper lobe being relatively constant in shape. In all examples the opening of the vas deferens was beneath the median lobe of the vergic papilla, the two lower and lateral lobes serving as a channel for sperm transfer.

No systematic significance should be given to the great size variation shown by the individual small sets measured (table XLVIII). Because of the depressed spire, already crowded ribbing, regular umbilical decoiling, and lack of body whorl descension, separation of adult from subadult shells is virtually impossible. Probably the specimens from Stations 113 and 127 are fairly close to typical adult size. The types are dis-



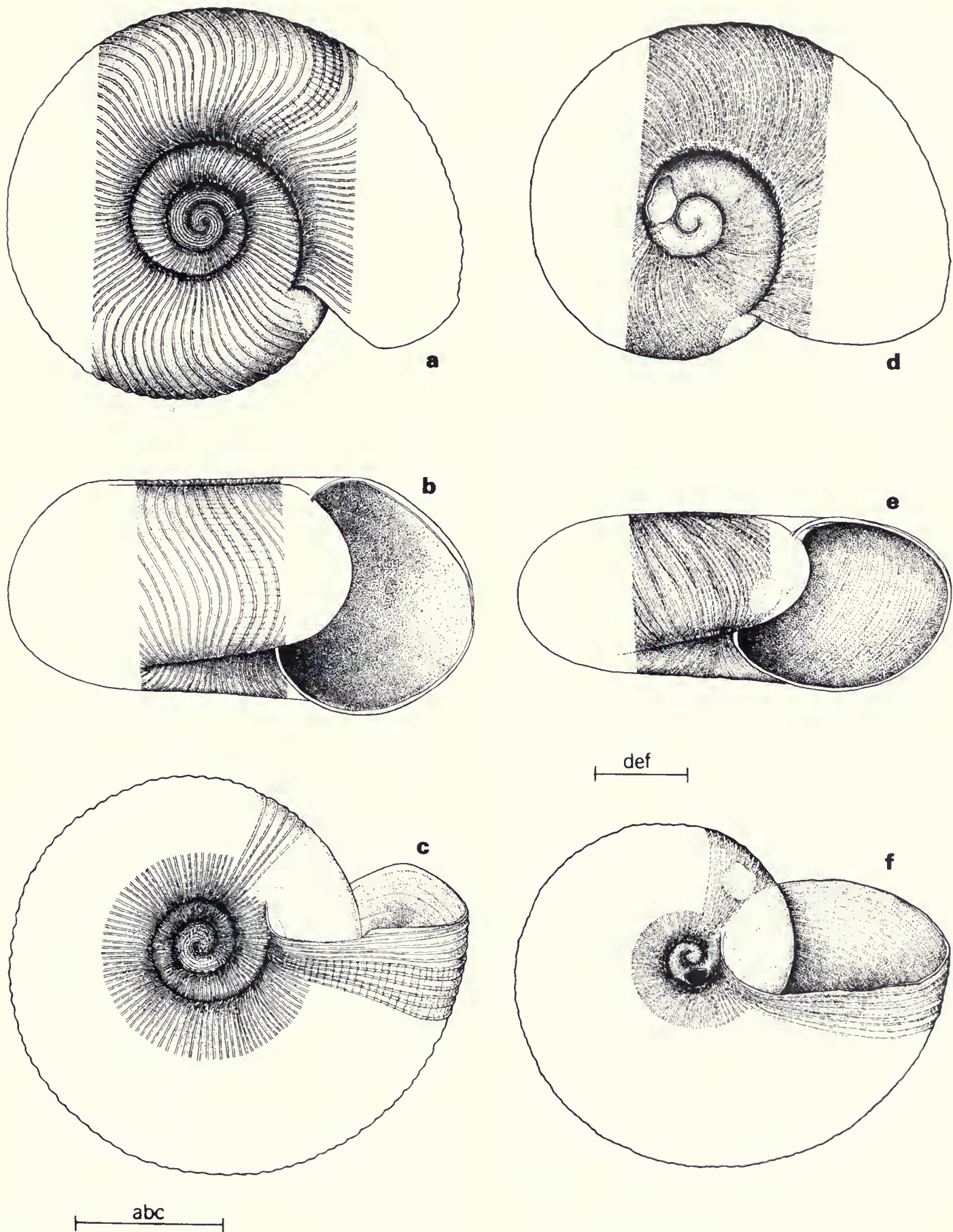


FIG. 89. a–c, *Kubaryiellus kubaryi* (Möllendorff). Ponape, Caroline Islands. Paratype. BPBM 87528 ex SMF; d–f, *Russatus nigrescens* (Möllendorff). Station 129A, Mt. Nanalaut, Ponape, Caroline Islands. BPBM 154521. Scale lines equal 1 mm. (MM).

tinctly smaller and more widely umbilicated than the Micronesian Expedition shells. This is not a size-correlated change, since almost certainly subadult shells from Station 140 agree in umbilical width with the other Micronesian Expedition shells. The latter were collected at higher elevations than the types (Möllerndorff, 1900, p. 101). The opposite variation is seen in *Russatus nigrescens* (table XLVIII), where the low elevation syntype specimens were much more narrowly umbilicated than the Micronesian Expedition upland shells. Further collections of both species are needed.

*Description of soft parts.*—Foot and tail long and slender, up to 3.75 mm. long, tapering posteriorly, broadly rounded at end, truncated in front. Sole undivided. Pedal grooves high on foot, pedal much stronger, both uniting above tail, but no caudal horn or mid-dorsal groove present. Slime network details not clear in available material. Head partly retracted in all specimens examined. Gonopore position not observed. Body color light yellow-white, without darker markings.

Mantle collar without glandular extension onto pallial roof. Anus (A) opening at inner edge of pneumostome, external ureteric pore (KX) opening well behind anus. Pallial region (fig. 90e) about 3.6 mm. from inner edge of mantle collar to apex of kidney. Lung roof clear, without granulations. Kidney (K) with 2 lobes, pericardial barely longer than heart, rectal arm about 2.2 mm. long, more than twice length of pericardial arm. Ureter (KD) with arms closely approximated, no lung roof visible between, tapering anteriorly. Heart (H) lying parallel to hindgut, about equal in length to pericardial kidney lobe. Principal pulmonary vein (HV) without obvious branching. Intestinal loop just above pallial cavity apex, hindgut (HG) reaching parietal-palatal margin just above pallial cavity apex.

Ovotestis (fig. 90f, G) one clump of 5–8 iridescent, very elongated acini, lying parallel to sides of whorls, located just above stomach apex, extending a fraction of a whorl. Hermaphroditic duct (GD) tightly convoluted apically and, in some specimens, just before talon, iridescent for most of length, inserting at base of talon head. Albumen gland (GG) short, compact. Talon (GT) partly buried in surface of albumen gland, head globose, shaft slender to carrefour. Prostate (DG) of narrow acini opening into groove on inner surface of uterus, acini variable in length. Uterus (UT) bipartite, upper chamber much more thin-walled and more slender than thick-walled lower chamber (fig. 90h).

Vas deferens (VD) thin-walled at first, becoming more muscular at penioviducal angle, loosely or not bound to side of penis, entering penial apex after passing through penial retractor muscle and traversing head of penis. Penial retractor (PR) very short, arising from diaphragm, inserting on head of penis after enfolding vas deferens. Penis (P) about 1.95–2.20 mm. long, club-shaped, covered by a thin muscle sheath, usually tapered basally (figured example bifoliated basally), internally (fig. 90g) with a trilobed vergic papilla (PV) through which vas deferens enters. Lower part of penis apparently with two simple to corrugated longitudinal pilasters that form one side of the papillate lower penial region. Atrium (Y) long and much more slender than penis base.

Free oviduct (UV) shorter than penis, wider apically and slightly expanded before joining spermathecal shaft. Spermatheca (S) with ovate head next to albumen gland, shaft slender to level of free oviduct, then greatly expanded with thick glandular walls. Vagina (V) elongated, slender, with weak internal pilasters. Free muscle system without unusual features. Salivary glands fused posteriorly above esophagus.

(Based on BPBM 157211–2, 5 extracted and partial specimens.)

### Genus *Russatus*, new genus

Shell very large, with less than  $3\frac{1}{2}$  very loosely coiled whorls. Apex and spire flat or slightly depressed, body whorl descending slightly. Apex macroscopically smooth, traces of fine spiral cording

visible under high magnification. Postnuclear whorls with irregular, very crowded, fine radial ribs with high periostacal extensions, on lower spire not separable from growth irregularities. Occasional microreticulation visible at  $96\times$  magnification. Umbilicus very narrow, V-shaped, regularly decoiling. Whorls compressed laterally above periphery and on basal margin, aperture strongly inclined from shell axis. No apertural barriers. Pallial cavity extending  $\frac{1}{4}$  whorl apically, kidney almost square, very thick in middle, rectal and pericardial arms equal in length. Apical genitalia not examined. Penial retractor muscle enfolding vas deferens before latter enters laterally on penis head through a simple pore. Expanded head of penis triangular, internally with a blind caecum lying at apex from opening of vas deferens to outer edge of expanded penis head, lower parts with circularly elongated glandular papillae on the walls. Spermatheca with basal part of stalk globularly expanded, vagina relatively long and much thicker than free oviduct.

*Type species.*—*Flammulina (Calymna) nigrescens* Möllerndorff, 1900.

Except for the Guam Island *Himeroconcha fusca* (fig. 105d–f), *Russatus nigrescens* is the largest Micronesian charopid. Its major distinguishing features are the reduced whorl count (table XLV), much looser coiling pattern (fig. 89d), great sculptural reduction, development of a square kidney (fig. 90a) that remains next to the hindgut, and the very peculiar caecum on the inner wall of the penis (fig. 90d). No Polynesian or Micronesian species is at all similar in shell coiling pattern, and the whorl count is lower than all known species. Only the minute and very tightly coiled *Microcharopa mimula* (fig. 33a–c) and the very high-spired *Ba humbugi* (fig. 74a–c) from Viti Levu, Fiji, come close in terms of whorl count. They differ markedly in coiling pattern, apical sculpture (*Microcharopa*, fig. 4a–d), and genital anatomy (*Ba*, fig. 75a–h).

The New Guinea endemic *Paryphantopsis* (Solem, 1970a, fig. 1a–c, shell, and fig. 2a–e, anatomy) is similar in whorl count, coiling pattern, major sculpture reduction, and size, but the similarities are convergent. In *Paryphantopsis* the pallial cavity has the kidney partly rotated from the hindgut, the arms of the ureter are separated at a  $60^\circ$  angle instead of being in contact, the principal pulmonary vein is noticeably branched, and the entire pallial cavity only occupies one-sixth whorl. *Paryphantopsis* has quite different terminal genitalia, there being an enlarged epiphallus with a prominent caecum, the penis with a verge and corrugated longitudinal pilasters, and the vaginal region being very short and swollen with thick glandular walls. *Russatus* lacks both an epiphallus and a verge. Species of *Paryphantopsis* have the umbilicus completely closed or at most a weak lateral crack, whereas the umbilicus of *Russatus nigrescens* is distinctly open.

Both genera have started the process of visceral hump reduction that can eventually lead to evolution of a "slug" genus, but the pallial cavity and genital structures indicate that they are not closely related.

Either *Kubaryiellus kubaryi* (fig. 90e–h) or *Trukcharopa trukana* (fig. 90i–j) might be compared with *Russatus nigrescens* as a possible ancestral type. The first has a large vergic papilla, very prominent stimulators, and the pallial cavity with very long rectal and much shorter pericardial kidney arms. *Truk-*



TABLE XLVIII. — LOCAL VARIATION IN KUBARYIELLUS AND RUSSATUS.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>Kubaryiellus</u>						
<u>kubaryi</u> BPBM 86245, SMF 165352-3	4	117.7±7.85 (105-132)	9.90±0.431 (9.15-10.64)	1.78±0.016 (1.74-1.81)	3.73±0.079 (3.59-3.95)	0.479±0.0094 (0.458-0.495)
Sta. 113 BPBM 157211-2	4	132.0±18.27 (108-168)	10.13±0.784 (9.34-11.70)	2.00±0.064 (1.88-2.14)	4.09±0.183 (3.68-4.57)	0.490±0.0159 (0.453-0.524)
Sta. 127 BPBM 154451-2	4	-----	-----	2.03±0.076 (1.88-2.24)	3.97±0.091 (3.71-4.14)	0.511±0.0102 (0.492-0.540)
Sta. 140 BPBM 157864	6	-----	-----	1.71±0.040 (1.58-1.84)	3.47±0.058 (3.36-3.72)	0.493±0.0068 (0.471-0.519)
<u>Russatus</u>						
<u>nigrescens</u> Pre-1900 SMF 165551-2, DMW MF8753	7	-----	-----	2.15±0.033 (2.01-2.27)	4.77±0.053 (4.57-5.00)	0.450±0.0072 (0.418-0.475)
In 1936 BPBM 154077,-403, -520, BPBM 156678	4	-----	-----	2.26±0.177 (1.92-2.68)	4.82±0.283 (4.37-5.56)	0.464±0.0125 (0.430-0.483)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	
<u>kubaryi</u> 86245	4	1 1/8-(4-4 1/4)	1.08±0.028 (1.02-1.15)	3.46±0.062 (3.36-3.64)	7	
Sta. 113	4	3/8-(4 1/8-4 1/2)	1.11±0.072 (0.99-1.32)	3.70±0.136 (3.48-4.06)	7.5±0.500 (6-8)	
Sta. 127	4	1/4-(4-4 1/2)	1.05±0.036 (0.95-1.12)	3.79±0.147 (3.53-4.21)	6.8±0.479 (6-8)	
Sta. 140	4	(3 7/8-4 1/8)	0.94±0.041 (0.82-1.09)	3.73±0.108 (3.43-4.12)	8.2±0.307 (7-9)	
<u>nigrescens</u> Pre-1900	3	(3-3 1/8)	0.35±0.040 (0.30-0.43)	14.22±1.38 (11.70-16.45)	----	
In 1936	3	1/4+(3 1/8-3 1/2)	0.62±0.054 (0.46-0.69)	7.92±0.685 (6.30-9.64)	REDUCED	

*charopa* has the penis without a vergic papilla, possesses a very unusual medial penial stimulator and agrees in pallial configurations with *Kubaryiellus*. Although their shell form appears intermediate between the more typical Trukcharopinae and *Russatus*, their anatomical features indicate no close affinity.

The name *Russatus*, meaning clothed in red, refers to the very dark color of the shell.

***Russatus nigrescens*** (Möllendorff, 1900). Figures 89d-f, 90a-d.

*Flammulina (Calymna) nigrescens* Möllendorff, 1900, J. Malacol., 7 (5), pp. 107-108, figs. 1-3—Naupilo, Ponape, Caroline Islands, at 100 m. elevation.

**Diagnosis.**—Shell very large, diameter 4.34-5.53 mm. (mean 4.81 mm.), with 3¼-3½ loosely coiled whorls. Apex and spire flat or very slightly depressed, last part of body whorl descending slightly, H/D ratio 0.418-0.482 (mean 0.455). Apical whorls with faint traces of spiral cords under high magnification, macroscopically smooth. Postnuclear whorls with irregular, extremely narrow and crowded, protractively sinuated radial ribs with lamellar extensions, becoming indistinguishable from growth irregularities shortly after apex. Occasional traces of microreticulation visible under 96× magnification. Umbilicus very narrow, broadly V-shaped, regularly decoiling,

contained 6.30-16.5 times (mean 10.6) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above, greatly compressed laterally above strongly rounded periphery and on basal margin. Aperture elongately ovate, compressed laterally above periphery and on basal margin, inclined almost 40° from shell axis. No apertural barriers.

*Russatus nigrescens* has the lowest whorl count and loosest coiling pattern of all Pacific Island Endodontidae and Charopidae. Its large size, tiny umbilicus, reduced apical sculpture, and very crowded, lamellar major radial sculpture immediately separate it from any Micronesian species.

**Description.**—Shell very large, with 3¼ very loosely coiled whorls. Apex and early spire flat, body whorl descending very slightly, H/D ratio 0.466. Apical whorls 1½, sculpture eroded with only faint traces of spiral cording visible in sutures. Postnuclear whorls with irregularly spaced radial ribs and growth threads plus a fine wavy spiral sculpture of riblets. Sutures moderately impressed, whorls flatly rounded above and on basal margin. Color dark purplish brown with occasional lighter patches becoming deep purple in the sutures and umbilicus. Umbilicus very narrow, greatly constricted by growth of periostracum, contained 16.45 times in the diameter. Aperture elongately ovate, flattened above periphery and on basal margin, inclined almost 35° from the shell axis. Height of lectotype 2.27 mm., diameter 4.87 mm.

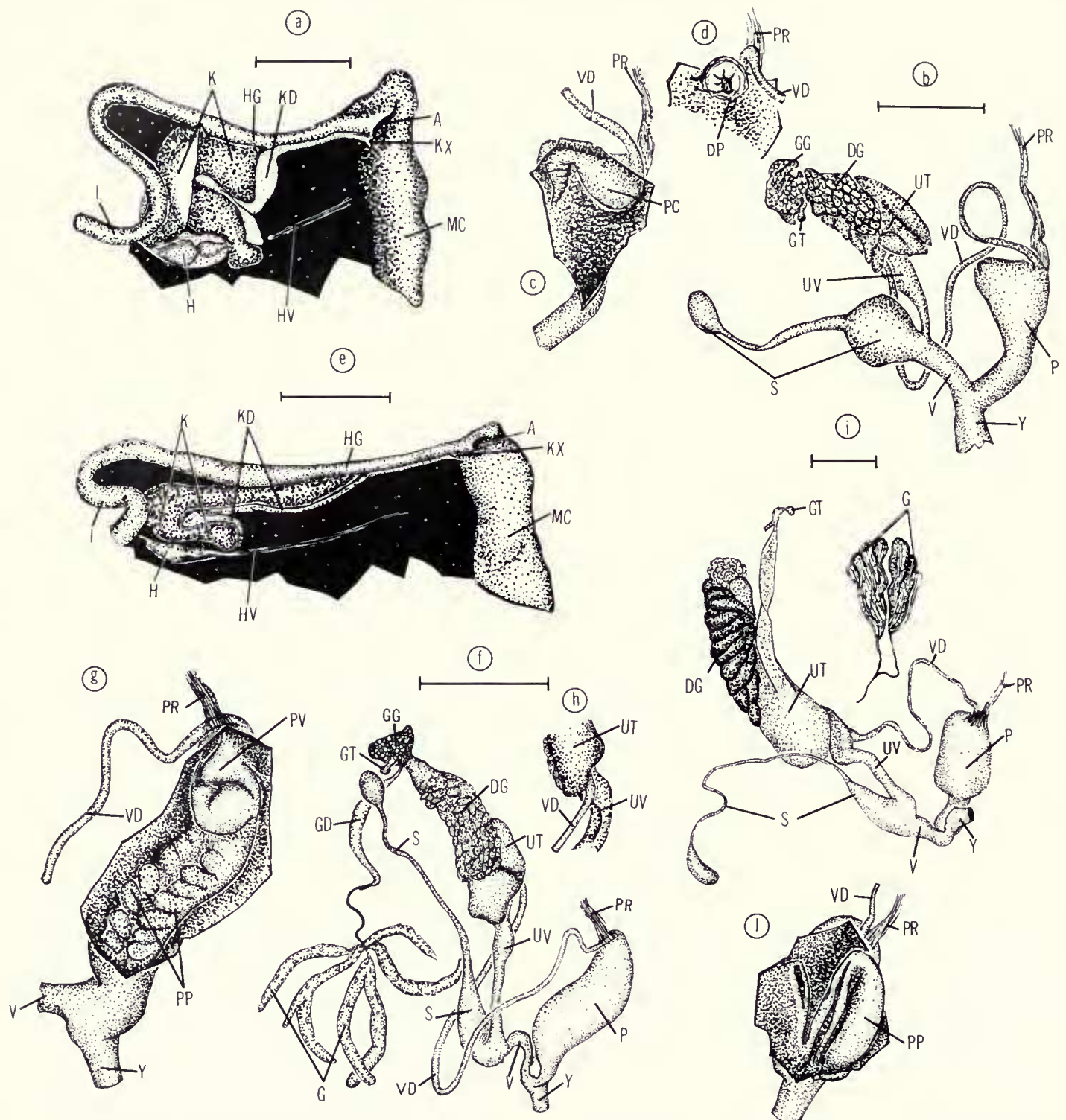


FIG. 90. Anatomy of *Russatus*, *Kubaryellus*, and *Trukcharopa*: a-d, *Russatus nigrescens* (Möllendorff). Station 129A, Ponape. BPBM 154522. a, pallial region, b, genitalia. c, interior of penis with caecum (PC) hiding vas opening. d, interior of penis showing relation of vas opening (DP) and pore of caecum; e-h, *Kubaryellus kubaryi* (Möllendorff). Station 113, Ponape. BPBM 157212. e, pallial region. f, genitalia. g, interior of penis. h, detail of prostate-uterus ending; i-j, *Trukcharopa trukana*, new species. Station A4, Moen Islet, Truk. BPBM 189263. i, genitalia; j, interior of penis. Scale lines equal 1 mm. (MO).

*Lectotype*.—Caroline Islands: Ponape, Naupilo, at about 100 m. elevation. Collected by Kubary. SMF 165551.

*Range*.—Ponape, Caroline Islands.

*Paratypes*.—SMF 165552.

*Material*.—Ponape (1 specimen, DMW): Mt. Tolotom (Station 92), from  $\frac{1}{4}$ – $\frac{3}{4}$  way up, near 800 ft. ele-

vation (2 specimens, BPBM 156678); Mt. Tolotom (Station 93),  $\frac{3}{4}$  way up, to summit at 1,200 ft. elevation on dead leaves (11 specimens, BPBM 154077–80); Mt. Nanalaut (Station 129A), from 1,900 ft. to summit, on ground (8 specimens, BPBM 154520–2); Mt. Kuporujō, near summit (Station 122) at 1,600–1,970 ft. elevation (2 specimens, BPBM 154403).



**Remarks.**—Only four of 23 specimens collected by the Micronesian Expedition were adult, and each came from a different station. Although the original collection was made at low altitude, 100 m., subsequent finds have been at higher elevations from widely scattered localities. The types are much more narrowly umbilicated than the more recently collected shells (table XLVIII), but I am uncertain as to the significance of this difference. Possibly subspecific differentiation is involved.

Suter (in Möllendorff, 1900, p. 108, figs. 1–3) illustrated the tail of a dried, then softened, individual, part of the jaw, and a portion of one radular half row. His classification of this species with *Flammulina* was a logical guess but is not supported by subsequent dissections. *Flammulina* shows major differences in pallial and genital anatomy (fig. 29a–j). The conchological similarities clearly are convergent.

*Russatus nigrescens* has fewer whorls, mean count  $3\frac{3}{8}+$ , than any Pacific Island endodontoid. The Fijian *Ba humbugi* has somewhat similar alteration in form, but clearly differs in its greatly elevated spire and anatomical structure (fig. 75a–h). *Ba humbugi* does have a mean whorl count of  $3\frac{3}{8}$ , but the pattern of coiling (fig. 74a) is very different.

**Description of soft parts.**—Foot and tail about 5.5 mm. long, tapering gradually from visceral stalk to narrowly rounded tip, truncated anteriorly. Sole undivided. Pedal groove very prominent, suprapedal much weaker, both uniting over tail with marked indentations, no caudal horn or middorsal groove developed. Slime network weak, more distinct posteriorly, backward slanting grooves on tail. Head projecting slightly in front of foot. Ommatophores very long. Gonopore located in front of and slightly below right rhinophore. Body color yellow-white, without darker markings.

Mantle collar (MC) rather narrow, thick, no glandular extension onto pallial roof. Anus (A) and external ureteric pore (KX) opening side by side just inside pneumostome, with anal opening slanted. Pallial region (fig. 90a) extending apically about  $\frac{1}{4}$  whorl, length about 1.7–1.9 mm. Lung roof clear, without granulations. Kidney (K) squarish, about 1.25–1.45 mm. long, compact, much thicker in middle with a sharp ridge, narrowing abruptly toward anterior, much more gradually posteriorly, rectal and pericardial arms equal in length, shape irregular in outline. Ureter (KD) with primary and secondary arms compacted and sinuated between kidney lobes, quite variable in width, becoming narrow along hindgut. Heart (H)  $\frac{1}{4}$  length of kidney, slightly angled from hindgut. Principal pulmonary vein (HV) unbranched, inconspicuous. Hindgut (HG) continuing along parietal-palatal margin for short distance above pallial cavity apex.

Apical genitalia not seen. Albumen gland (fig. 90b, GG) very irregular in shape, with large acini. Talon (GT) small, head globular, with a short shaft to slightly more expanded carrefour. Prostate (DG) of few long acini entering groove on inner surface of uterus, lower rows partly covered by uterine chamber folds. Uterus (UT) bipartite, lower chamber very large, completely folded, with thick glandular walls.

Vas deferens (VD) very slender and with thin walls at first, becoming thicker and with muscular walls long before reflexion at penioviducal angle, not attached to penis during ascent, entering head of penis laterally after passing through penial retractor muscle (PR), which is fairly long and arises from diaphragm. Penis (P) a little less than 1.4 mm. long, apex very broad, upper  $\frac{2}{3}$  roughly triangular, lower 3rd a simple tube equal in diameter to free oviduct. Interior of penis (fig. 90c–d) with a blind-end muscular tube (PC) situated transversely at apex, opening muscular and puckered (fig. 90d), vas deferens opening (DP) at attached base of caecum. Lower

portions minutely papillose and glandular, papillae elongate and circularly arranged. Atrium (Y) short and rather broad.

Free oviduct (UV) sharply tapering to union with spermatheca. Spermatheca (S) with small, ovate head next to albumen gland, shaft slender to near base of uterus, becoming grossly globular with very thick muscular and glandular walls. Vagina (V) equal in length to or slightly longer than free oviduct, wider in diameter. Free muscle system without unusual features, tentacular retractors remain separate and unite with tail fan at columellar muscle.

(Based on BPBM 154522, several partial specimens.)

### Genus *Roimontis*, new genus

Shell of average size, with 4 overlapping whorls. Apex and spire deeply sunken beneath level of body whorl, last 3rd of body whorl with looser coiling. Apical sculpture of 6–7 very prominent spiral cords. Postnuclear sculpture of narrow, protractively sinuated, widely spaced radial ribs, about 6.6/mm. on body whorl. Microsculpture of fine radial riblets, finer spirals, and prominent secondary spiral grooves. Umbilicus shallow, narrow, V-shaped, margins rounded. Whorls very strongly flattened laterally above periphery with compressed lower palatal and basal margin, aperture inclined about  $20^\circ$  from shell axis. Parietal wall with 2 threadlike ridges extending about  $\frac{3}{16}$  of a whorl. No columellar or palatal barriers. Anatomy unknown.

**Type species.**—*Roimontis tolotomensis*, new species.

Despite the absence of anatomical data, I have no hesitation in describing this as a new genus. The deeply sunken apex and spire (fig. 91a–b), presence of secondary spiral grooves rather than cords, and development of two very low parietal barriers are highly distinctive. *Kubaryellus* (fig. 89a–c) has a much less sunken apex, lacks the parietal barriers, has secondary spiral cording, is much larger and more widely umbilicated, but is the most similar species in shell structure. Compared with the minor shell differences between *Trukcharopa trukana* (fig. 63d–f) and *Sinployea kusaieana* (fig. 63a–c), these are major changes. With the pattern of generic differentiation seen in the other Micronesian species, existence of these several major conchological changes is acceptable as indicating generic level separation. On the basis of the dark shell color, similarity in sculpture to the other Caroline Island species without an epiphallus, and relatively low whorl count, I tentatively classify this with the Trukcharopinae. I suspect that its anatomy will show marked differences from all of the above.

*Roimontis* refers to the habitat of this species on the slopes of Mt. Tolotom, sometimes known as Roi Mountain.

### *Roimontis tolotomensis*, new species. Figure 91a–c.

**Diagnosis.**—Shell small, diameter 2.65–2.91 mm. (mean 2.78 mm.), with 4 very tightly coiled and overlapping whorls. Apex and spire deeply sunken, last quarter of body whorl beginning to descend slightly, but not reaching level of first part of body whorl, H/D ratio 0.523–0.525 (mean 0.524). Apical sculpture of 6–7 (mean 6.5) prominent spiral cords whose interstices are 3–4 times their width. Postnuclear whorls with high, lamellar, very narrow, almost vertically sinuated radial ribs, 57–58 (mean 57.5) on the body whorl, whose interstices are 4–8 times their width. Ribs/mm. 6.27–7.01 (mean 6.64). Microsculpture of fine radial riblets, 5–12 between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with a prominent secondary sculpture of widely spaced spiral grooves that become more crowded near sutures and on shell base. Umbilicus relatively shallow, V-shaped, regularly decoiling, contained 3.81–



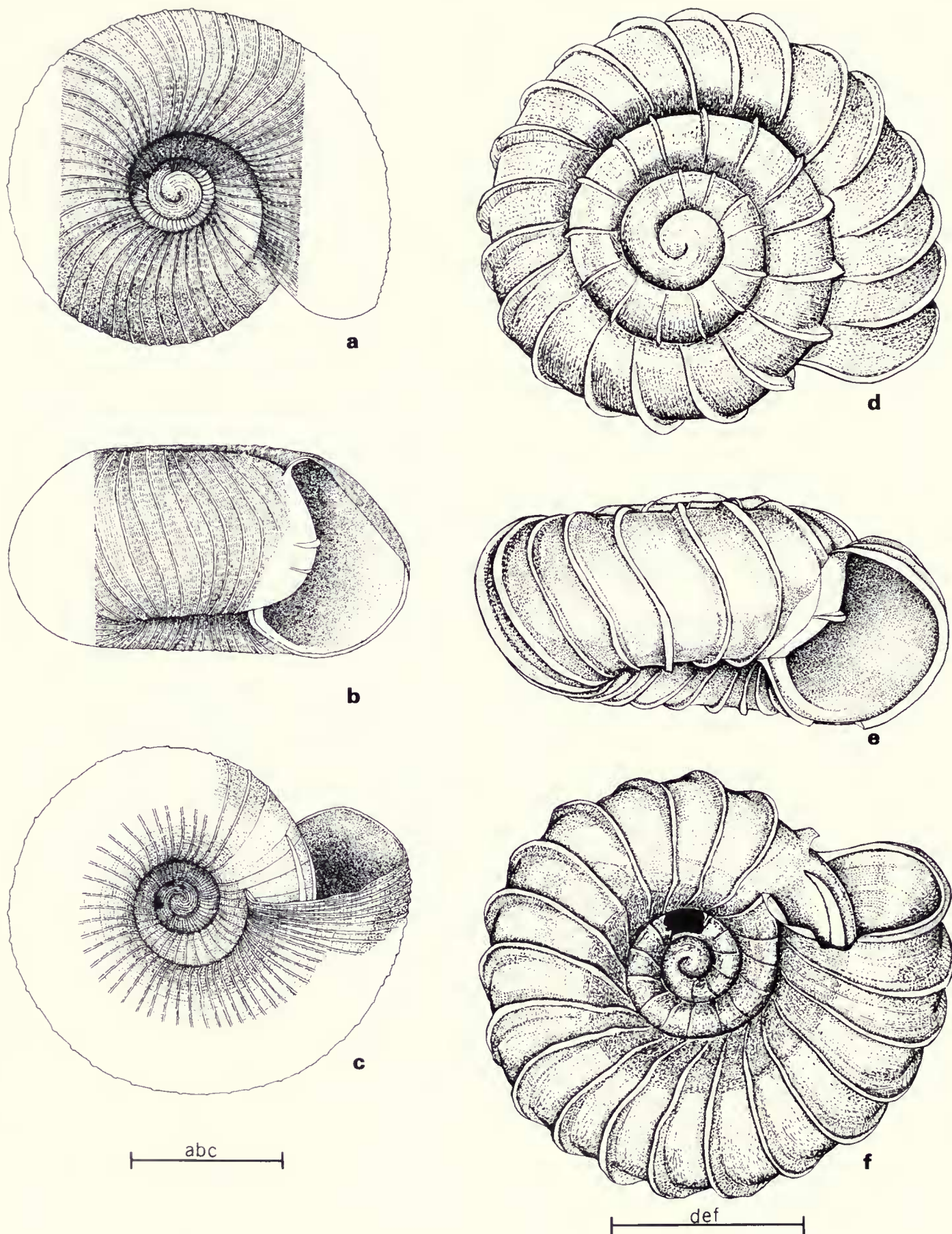


FIG. 91. a–c, *Roimontis tolotomensis*, new species. Station 93, Mt. Tolotom, Caroline Islands. Holotype. BPBM 154081; d–f, *Palikirus cosmetus*, new species. Station 139, Palikir, Ponape, Caroline Islands. Holotype. BPBM 157798. Scale lines equal 1 mm. (a–c, MM; d–f, SH).



4.00 times (mean 3.91) in the diameter, margins evenly rounded. Sutures deep, whorls shouldered above, strongly flattened laterally above rounded periphery, moderately compressed basally, with evenly rounded basal margin. Aperture subtriangular, strongly compressed and flattened laterally with downwardly moved periphery, inclined about  $15^{\circ}$ – $20^{\circ}$  from shell axis. Parietal barriers 2, threadlike ridges extending posteriorly less than  $\frac{3}{8}$  of a whorl: upper weakly raised medially, located just above periphery; 2nd a very low cord about  $\frac{1}{3}$  of way to parietal-columellar margin, not raised on any portion.

Other species with a depressed apex include *Kubaryiellus kubaryi* (Möllendorff) (fig. 89a–c), which is much larger, has many more radial ribs (table XLV), and lacks the parietal barriers; and *Russatus nigrescens* (fig. 89d–f), which is much, much larger, lacks apertural barriers, and has a reduced whorl count. *Palline micramyla* (fig. 95c–e) is much smaller, has secondary spiral cording, not grooving, a slightly raised apex, and much more crowded and numerous radial ribs.

*Description*.—Shell small, with 4 strongly overlapping whorls. Apex deeply sunken, last whorl strongly overlapping former and globosely swollen, descending slightly, H/D ratio 0.525. Embryonic whorls  $1\frac{1}{2}$ , with 7 quite prominent spiral cords. Postnuclear whorls with thin, lamellate, slightly protractively sinuated radial ribs, 58 on the body whorl, whose interstices are 5–8 times their width. Microsculpture of fine, widely spaced radial riblets, crossed by very low and indistinct spiral riblets, plus secondary sculpture of relatively prominent, broadly rounded, spiral grooves. Sutures inset, with whorls strongly shouldered above, distinctly flattened laterally above periphery with moderately flattened basal margin. Umbilicus relatively shallow, cup-shaped, contained 3.81 times in the diameter. Color light reddish yellow-brown. Aperture elongately ovate, strongly flattened laterally above periphery with gently rounded basal margin, inclined about  $15^{\circ}$  from the shell axis. Parietal wall with 2 threadlike barriers extending almost  $\frac{3}{8}$  of a whorl, the upper slightly raised in middle  $\frac{3}{8}$ . Height of holotype 1.38 mm., diameter 2.63 mm.

*Holotype*.—Caroline Islands: Ponape, Station 93, three-quarters of the way to summit of Mt. Tolotom at about 1,200 ft. elevation. Collected by Yoshio and Kiyoko Kondo on February 15, 1936. BPBM 154081.

*Range*.—Mt. Tolotom, Ponape, Caroline Islands.

*Paratype*.—(Station 92) one-quarter to three-quarters of the way up Mt. Tolotom at 800 ft. elevation (1 specimen, BPBM 156681).

*Remarks*.—At first glance *Roimontis tolotomensis* could be mistaken for a juvenile example of *Kubaryiellus kubaryi*, but the presence of two parietal barriers, the much more deeply sunken apex, much smaller size at the same whorl count, and much more widely spaced radial ribbing easily distinguish the two species.

Both known examples of *Roimontis tolotomensis* were collected on the slopes of Mt. Tolotom between 800 and 1,200 ft. elevation. The shells are adult, with the last third of the body whorl beginning to descend from the very overlapping coiling pattern of previous whorls, but in neither case does the apertural upper edge fall below the level of the penultimate whorl.

Although the one specimen (BPBM 154081) was listed in the BPBM catalogue as having been collected

alive, no anatomical material of this species could be located.

### Genus *Palikirus*, new genus

Shell very small, with 3% to about 4 rather tightly coiled whorls. Apex and spire barely to slightly elevated, body whorl descending more rapidly. Apical sculpture of very fine and widely spaced spiral cords. Postnuclear sculpture of very large, prominent, protractively sinuated radial ribs, usually quite widely spaced. Microsculpture of fine radial riblets, finer spiral riblets, and relatively prominent secondary spiral cords. Umbilicus moderately open, margins rounded to angulated. Parietal wall with (*cosmetus*) or without (*ponapicus*) a medial, low, bladeliike barrier. Columellar and palatal walls without barriers. Pallial region extending  $\frac{1}{2}$  whorl apically with rectal kidney arm crossing hindgut and extending onto parietal wall, about 30% longer than pericardial kidney arm. Ovotestis not seen. Hermaphroditic duct not convoluted. Vas deferens passing through penial retractor muscle before entering penis through a simple pore. Penis with an expanded head, internally having weak longitudinal pilasters to level of an external constriction that marks presence of a globose, muscular-walled stimulatory pad, puckered near point of attachment to wall. Lower portion of penis with minutely papillose glandular walls. Spermathecal shaft markedly expanded on lower section, free oviduct relatively long, vagina short.

*Type species*.—*Palikirus cosmetus*, new species.

Discussion of the anatomical differences between *Palikirus* and *Jokajdon* is given under the latter generic name. Conchologically, they are very distinctive, the few extremely high and large major radial ribs of *Palikirus cosmetus* (fig. 91d–f) contrasting greatly with the low and crowded radial ribbing of the two *Jokajdon* (fig. 92a–f). Besides the obvious ribbing differences, the larger size, fewer whorls, looser coiling, and only single parietal barrier of *Palikirus* distinguish the two genera. *Roimontis tolotomensis* (fig. 91a–c) is the only Micronesian species that might be confused with *P. cosmetus*, and then only on the basis of having two weak parietals, comparatively few radial ribs, and a moderately wide umbilicus. It has the apex and spire deeply depressed, secondary spiral grooving rather than cords, the shell is very strongly flattened laterally above the periphery, and is distinctly larger in size. *Semperdon kororensis* (fig. 98a–c) has superficially similar ribbing, but is much larger in size, has a closed umbilicus, and numerous complex apertural barriers besides a very different penial structure.

Inclusion of *Charopa ponapica* Möllendorff, 1900, in this genus is purely for convenience. The holotype and only known example of that species may not be fully adult. Although it shows more similarities to *P. cosmetus* than to any other Micronesian species, these similarities in sculpture and form could be convergent. Until living specimens can be collected and dissected, classification in *Palikirus* is a reasonable positioning for identification purposes.

The name *Palikirus* is taken from the occurrence of the type species near Palikir in the Jokaj District of Ponape.

***Palikirus cosmetus*, new species.** Figure 91d–f.

*Diagnosis*.—Shell very small, diameter 2.17–2.58 mm. (mean 2.40 mm.), with 3%–4 normally coiled whorls. Apex and spire mod-

TABLE XLIX. - LOCAL VARIATION IN PALIKIRUS AND JOKAJDON.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER	H/D RATIO
<u>Palikirus cosmetus</u>						
Sta. 139 BPBM 157798-9	5	18.8±0.489 (18-20)	2.53±0.074 (2.29-2.71)	1.19±0.024 (1.12-1.27)	2.37±0.061 (2.17-2.50)	0.504±0.0046 (0.487-0.515)
<u>Jokajdon callizonus</u>						
TYPES: SMF 165700-1, BPBM 86246	3	129.3±15.93 (99-153)	20.12±1.229 (17.71-21.73)	0.92±0.071 (0.79-1.04)	2.03±0.135 (1.78-2.24)	0.450±0.0063 (0.444-0.463)
Sta. 93, BPBM 9688	3	127.3±9.92 (109-143)	18.57±1.181 (16.22-19.89)	0.97±0.041 (0.92-1.05)	2.18±0.056 (2.11-2.29)	0.445±0.0087 (0.430-0.460)
Sta. 118, BPBM 154161, BPBM 157282	7	-----	-----	0.88±0.013 (0.84-0.94)	1.96±0.026 (1.86-2.04)	0.450±0.0079 (0.428-0.478)
<u>Jokajdon tumidulus</u>						
TYPES: SMF 165702-3, BPBM 86247	12	99.1±4.18 (79-123)	13.14±0.485 (10.35-15.97)	1.35±0.031 (1.22-1.56)	2.40±0.040 (2.20-2.63)	0.561±0.0053 (0.532-0.594)
Sta. 146, Jokaj, Id. BPBM 157984-5	5	114.8±7.62 (92-140)	14.58±0.500 (13.78-16.45)	1.46±0.094 (1.12-1.64)	2.50±0.113 (2.09-2.71)	0.583±0.0126 (0.535-0.606)
Sta. 132 BPBM 157513-7	11	62.8±5.75 (39-95)	10.04±1.097 (5.80-16.18)	1.20±0.021 (1.09-1.28)	2.03±0.042 (1.81-2.20)	0.594±0.0061 (0.563-0.631)
Sta. 133 BPBM 157566-7	4	97.3±2.96 (89-105)	13.71±1.082 (11.56-16.54)	1.30±0.082 (1.10-1.48)	2.28±0.096 (2.02-2.45)	0.570±0.0130 (0.545-0.604)
Sta. 93 BPBM 154082	6	REDUCED	REDUCED	1.21±0.0130 (1.18-1.27)	2.05±0.018 (1.97-2.11)	0.592±0.0057 (0.571-0.608)
Sta. 95 BPBM 156730-1	6	REDUCED	REDUCED	1.30±0.0570 (1.25-1.48)	2.12±0.040 (2.01-2.30)	0.615±0.0083 (0.585-0.642)
		WHORLS	UMBILICUS	D/U RATIO	APICAL RIBS	
<u>cosmetus</u>						
Sta. 139	3	3 3/4+(3 5/8-3 7/8)	0.69±0.031 (0.63-0.79)	3.46±0.084 (3.16-3.67)	12.3±0.479 (11-13)	
<u>callizonus</u>						
TYPES	4	3/8(4 1/8-4 3/4)	0.66±0.045 (0.58-0.72)	3.06±0.029 (3.00-3.09)	8.3±0.067 (7-9)	
Sta. 93	4	1/2+(4 1/2-4 3/4)	0.72±0.025 (0.69-0.77)	3.01±0.044 (2.96-3.10)	8.3±0.034 (8-9)	
Sta. 118	4	1/2-(4 1/4-4 1/2)	0.66±0.014 (0.61-0.71)	3.00±0.077 (2.84-3.27)	8.0±0.258 (7-9)	
<u>tumidulus</u>						
TYPES	4	3/8+(4 1/8-4 3/4)	0.67±0.023 (0.54-0.82)	3.63±0.081 (3.19-4.18)	10.2±0.250 (9-11)	
Sta. 146	4	1/2+(4 1/8-5)	0.67±0.027 (0.59-0.71)	3.77±0.082 (3.53-3.90)	8.8±0.250 (8-9)	
Sta. 132	4	1/8+(3 7/8-4 1/4)	0.55±0.018 (0.48-0.64)	3.70±0.062 (3.28-3.94)	9.3±0.289 (8-11)	
Sta. 133	4	1/4(4 1/8-4 1/2)	0.65±0.016 (0.61-0.67)	3.50±0.166 (3.00-3.70)	9.7±0.334 (9-10)	
Sta. 93	4	1/4+(4 1/4-4 3/8)	0.60±0.022 (0.51-0.67)	3.46±0.113 (3.03-3.87)	9.3±0.211 (9-10)	
Sta. 95	4	3/8-(4 1/4-4 1/2)	0.60±0.022 (0.53-0.67)	3.55±0.151 (3.12-4.12)	9.0±0.516 (8-11)	

erately and evenly elevated, body whorl descending more rapidly, spire protrusion less than ¼ body whorl width, H/D ratio 0.487-0.542 (mean 0.510). Apical sculpture of 10-13 (mean 11.8) very fine spiral cords. Postnuclear whorls with extremely high, prominent, broadly U-shaped, strongly protractively sinuated radial ribs, 17-21 (mean 18.9) on the body whorl, whose interstices are 5-8 times their width. Ribs/mm. 2.29-2.71 (mean 2.51). Microsculpture of very fine radial riblets, more than 20 between each pair of major ribs, crossed by much finer and slightly more crowded spiral riblets, with an intermixture of crowded secondary spiral cords equal in size to microradials. Umbilicus broadly V-shaped, regularly decoiling, contained 3.14-3.67 (mean 3.44) times in the diameter, margins shouldered to

angled. Sutures impressed, whorls evenly rounded to slight flattening laterally above periphery, evenly rounded outer margin, slightly compressed lower palatal wall with angled baso-columellar margin. Aperture ovate, compressed laterally above periphery, inclined about 30° from shell axis. Parietal wall with a single low, bladeliike, medial barrier extending posteriorly almost ¼ whorl, minutely serrated above, evenly elevated for entire length until last ¼ whorl, with sharp to gradual anterior descension. No columellar or palatal barriers.

*Palikirus cosmetus* differs from *P. ponapicus* by its fewer, larger radial ribs, more crowded secondary spi-



ral cording, wider umbilicus, more apical cords, and possession of a parietal barrier. All other Caroline and Palau species have much finer and more crowded radial ribbing or many apertural barriers (*Semperdon kororensis*).

*Description*.—Shell very small, with 3% normally coiled whorls. Apex and spire evenly elevated, last whorl descending moderately, H/D ratio 0.487. Embryonic whorls 1½, sculpture of 13 relatively wide spiral cords. Postnuclear whorls with sculpture of very high, U-shaped, strongly protractively sinuated, widely spaced radial ribs, 18 on the body whorl, whose interstices are 4–6 times their width. Microsculpture of equally spaced radial and spiral riblets, the spiral slightly less prominent, plus obscure secondary spiral cording. Sutures deep, whorls evenly rounded above, somewhat flattened laterally above and below periphery with strongly rounded and slightly shouldered basal margin. Umbilicus broadly V-shaped, regularly decoiling, contained 3.45 times in the diameter. Color very light reddish yellow-brown. Aperture ovate, flattened laterally above and below periphery and on umbilical margin, inclined about 30° from shell axis. Parietal wall with 1 ridgelike barrier, slightly expanded above, extending almost ¼ whorl. Height of holotype 1.22 mm., diameter 2.50 mm.

*Holotype*.—Caroline Islands: Ponape, Station 139, Palikir, Jokaj District, at 600–900 ft. elevation. Collected on a dead tree by S. Ito and Yoshio Kondo on March 14, 1936. BPBM 157798.

*Range*.—Ponape, Caroline Islands.

*Paratypes*.—Ponape: Palikir (Station 139), Jokaj District, at 600–900 ft. elevation (4 specimens, BPBM 157798–9); west side of Mt. Tolotom (Station 91) at 1,000–1,500 ft. elevation (1 specimen, BPBM 154004); Palikir (Station 137), more than ¼ mile south of school at 450 ft. elevation (1 specimen, BPBM 157730); Palikir (Station 140), Mt. Tamantamansakir at 1,000–1,250 ft. elevation (1 specimen, BPBM 157865).

*Remarks*.—Although *Palikirus cosmetus* is very similar in sculpture to the Hawaiian *Cookeconcha stellulus* (Gould) (see Solem 1976b, p. 218, fig. 93), the two species obviously differ in apical sculpture and apertural barriers. The Palau Island *Semperdon kororensis* has very similar sculpture but is much larger and has numerous large barriers (fig. 98b).

The name *cosmetus*, from the Greek meaning “adorned,” refers to the spectacular nature of the radial ribbing.

Dissection of this species was accomplished during a period when I was without an illustrator. It was not possible to figure the genitalia or the pallial cavity because of the complicated structure and minute size.

*Description of soft parts*.—Foot and tail much less than shell diameter in length, tapering posteriorly. Pedal grooves and slime network typical. Gonopore in normal position. Body color yellow-white, without darker markings. Mantle collar thin, rather long, without glandular extension onto pallial roof. Anus opening very slightly anterior of external ureteric pore.

Pallial region extending ½ whorl apically. Lung roof clear, without granulations. Kidney typically bilobed, rectal arm about 1.3 mm. long, crossing hindgut and extending onto parietal wall, pericardial arm much shorter, less than 1 mm. from base to tip. Ureter tightly compacted between arms of kidney, portion along hindgut only slightly narrower than hindgut. Heart about ¾ length of pericardial kidney arm, lying parallel to hindgut. Principal pulmonary vein large, unbranched. Hindgut without unusual features.

Ovotestis not seen. Hermaphroditic duct a rather short, thick, iridescent tube, slowly tapering apically, strongly constricted before

reflexing into albumen gland and continuing apical to talon. Albumen gland short and compact, acini quite small. Talon with an ovate head and short stalk that leads into a much larger carrefour. Union of hermaphroditic duct apparently near junction of talon stalk and carrefour, but exact relationship not determined. Prostate of 4 very large acini opening into groove on inner uterine wall. Uterus bipartite, lower chamber expanded and with thick, glandular walls.

Vas deferens a slender tube, slightly expanded at penioviducal angle, becoming slender again during ascension alongside penis, entering head of penis after passing through penial retractor muscle fan. Penial retractor long, arising from diaphragm, attached to head of penis after enfolding vas deferens. Penis with expanded head of 0.3 mm. in length, followed by a much shorter, narrow tube. Head portion with a supramedial constriction externally. Internally the upper section of penis head with numerous narrow longitudinal pilasters on the muscular wall, vas deferens entering apex with no special vergic papilla formed. Lower part with a huge, globular pilaster with smoothly muscled surface, deeply creased near point of attachment on one side, with 3 or 4 different creases radiating from a central point. Free wall of lower chamber minutely papillose with glandular tissue. Atrium short, rather narrow.

Free oviduct about 0.6 mm. long, distinctly shorter than prostate-uterus, about ¾ diameter of expanded spermathecal shaft, with longitudinal pilasters. Spermatheca with elongately oval head lying next to albumen gland, slender shaft lying next to prostatic acini, becoming grossly expanded near origin of vas deferens to union with free oviduct, expanded portion with thick walls. Vagina short, tapering rapidly from glandularized apical section to atrium.

(Based on BPBM 157799, 2 partial examples.)

### *Palikirus ponapicus* (Möllendorff, 1900)

*Charopa ponapica* Möllendorff, 1900, J. Malacol., 7 (5), p. 110—Ponape, Caroline Islands.

*Description*.—Shell very small, with 3% normally coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending a little more rapidly, H/D ratio 0.454. Apical whorls 1%, sculpture partially eroded with traces of about 9 narrow, widely spaced, major spiral cords. Postnuclear whorls with rounded, prominent, protractively sinuated radial ribs, about 46 on the body whorl, whose interstices are 3–5 times their width. Microsculpture mostly obscured by fungal growths, but on portions visible as a fine network of co-equal spiral and radial riblets with a secondary sculpture of narrow, relatively widely spaced spiral cords. Sutures deep, whorls strongly rounded above, slightly flattened laterally above periphery and on basal margin. Umbilicus V-shaped, regularly decoiling, contained 4.00 times in the diameter with evenly rounded margins. Color very light reddish yellow-horn. Aperture ovate, slightly flattened laterally above periphery and on basal margin, inclined about 15° from the shell axis. Height of holotype 0.99 mm., diameter 2.17 mm.

*Holotype*.—Caroline Islands: Ponape. Collected by Quadras. SMF 165354.

*Range*.—Ponape, Caroline Islands.

*Remarks*.—Unfortunately, the microsculpture of the holotype and only specimen seen of *Palikirus ponapicus* is partially obscured by fungal growths. Despite this, the appearance is unmistakable, and *P. ponapicus* cannot be confused with any other Caroline Island species.

The relatively few major radial ribs, 46 on the body whorl, are lower and more closely spaced, ribs/mm. 6.74, than in *P. cosmetus*, which has only 17–21 major ribs that are widely spaced, 2.29–2.71 ribs/mm. The latter has a wider (mean D/U ratio 3.44) umbilicus and possesses a single parietal barrier that extends posteriorly for one-quarter whorl.

No specimens of *P. ponapicus* were obtained by members of the Micronesian Expedition. The holotype

was found in "bags of vegetable mould from the bush." These were taken "in the neighbourhood of the Spanish settlement on Ponape" by a German trader, Etscheid (Möllendorff, 1900, p. 101).

### Genus *Jokajdon*, new genus

Shell very small, with 4%–4½ very tightly coiled whorls. Apex and early spire flat or barely protruding, spire not or sharply descending. Apical sculpture with variable number of fine spiral cords. Postnuclear sculpture of prominent, narrow, slightly protractively sinuated radial ribs, usually crowded, sometimes widely spaced or greatly reduced. Microsculpture of fine radial riblets, finer spiral riblets, and prominent secondary spiral cords. Umbilicus moderately to widely open, walls rounded or flattened, margins strongly rounded to distinctly shouldered. Periphery rounded, with slight to very strong lateral flattening. Parietal barriers 2, with or without accessory blade on 1st, variable in length. Columellar wall with a low knob to high barrier. Palatal barriers 3, variable in height and degree of twisting, with 3–6 accessory lamellae. Pallial region with pericardial kidney arm greatly reduced, rectal arm enlarged, covering hindgut and extending down parietal wall, total length of pallial cavity about ¾ whorl. Genitalia with single clump of very few alveoli in ovotestis, hermaphroditic duct not convoluted. Penial retractor muscle very long, arising on diaphragm, inserting directly onto head of penis, vas deferens inserting on side of penis head just below muscle insertion. Penis variable in length, bitapered from middle, internally with weak longitudinal pilasters to middle, plus a *Sinployea*-type medial stimulatory pad just below middle. A separate muscle strand from the columellar retractor inserts directly onto penioviducal angle. Vagina very long, base of spermathecal shaft not expanded.

*Type species.*—*Endodonta (Thaumatodon) callizona* Möllendorff, 1900.

Several features in the anatomy of *Jokajdon* (fig. 93a–d) are highly unusual in relation to the other Micronesian Charopidae. The total absence of broad expansion for the spermathecal shaft is unique to these two species. In having the vas deferens insert laterally on the penis head just below the penial retractor union with the penis, *Jokajdon* differs considerably from most Micronesian genera. All those that lack an epiphallus, *Palikirus*, *Palline*, *Russatus*, *Kubaryellus*, and *Trukcharopa*, have the vas deferens crossing the penis head and passing through the penial retractor muscle before entering the penis. A comparatively simple rotation of the penis head in relation to the muscle insertion could change one condition to the other, but the division into five genera with the transverse passage of the vas deferens and one without is a remarkable split. Shortening of the pericardial kidney arm and extension of the rectal kidney arm onto the parietal wall is carried further in *Jokajdon* than in any Pacific Island species.

Internal penis structure of *Jokajdon* is most similar to that seen in *Palikirus cosmetus*. Both genera have the vas deferens opening through a simple pore and with longitudinal pilasters, but in *Palikirus* the penial stimulator is a huge globular pad with a puckered remnant of a "pocket," whereas in *Jokajdon* the pocketed stimulator is very close to the type seen in *Sinployea*. Probably the differences are exaggerated by character displacement, since *P. cosmetus* and *J. tumidulus* were collected at three of the four stations

from which *P. cosmetus* was taken. Gross enlargements of the penial pilaster in *Jokajdon* might account for this difference, but the gross spermathecal expansion, short vagina, enfolding of the vas deferens by the penial retractor, and absence of a special muscle on the penioviducal angle are major anatomical differences that suggest generic separation. *Palikirus cosmetus* with its single parietal barrier, very few and large radial ribs, slanted aperture, and reduced whorl count is conchologically very different in appearance.

Dissection of the two *Jokajdon* was very difficult, the large and sinuated apertural barriers having produced numerous distortions in the lower pallial and midgenital organs during the many years in preservative. The parts were mushy, and some apical organs had not been preserved, probably through failure of the preservative to penetrate rapidly enough past the pallial air bubble and barriers during initial field handling. The only anatomical distinction observed was the disparity in penial size, with the penis of *J. callizonus* being less than half the length seen in *J. tumidulus*. Studies of fresh material, probably by use of sections, will be required to see if penial size is the only distinction between the two species. Both dissected sets contained fully adult specimens so that no question of an age difference arises.

Conchological differences between the two species are covered in the diagnosis of *Jokajdon callizonus*. Besides the shape and size differences enumerated there, many barrier details are different (compare fig. 92b, e). Parietals are longer in *J. callizonus*, but an accessory lateral structure is found in *J. tumidulus*. *Jokajdon callizonus* has a huge columellar barrier that twists up to terminate on the parietal wall, whereas *J. tumidulus* has a low, triangular, knoblike ridge deeply recessed on the columellar wall. Less dramatic changes distinguish the pattern of palatal barriers in the two species, but comparison of the figures and descriptions show quite different details of form and proportions.

Insufficient detail is available for any decision to be made, but the possibility that *Jokajdon* is analogous to the Rapan *Rhysoconcha* should be kept in mind for future exploration. The latter clearly represents a group derived by size reduction (Solem, 1976b, pp. 255–258). The contorted palatal barriers of *Jokajdon* (figs. 92b, e) are comparable to the changes seen in *Rhysoconcha* (Solem, 1976b, p. 255, fig. 108a–b). Similarly, the single clump of very few and long alveoli in the ovotestis, lack of expansion in the spermathecal base, simplification of the vas-penis-retractor junction, and long vagina could be interpreted as resulting from differential change during size reduction. The addition of a special muscle to the penioviducal angle in *Jokajdon* may relate to the extreme degree of apertural constriction caused by the very large and complex barriers. Space between the parietals and palatals is so narrow that the animal may have great difficulty in effecting withdrawal of the foot and head into the shell. Neither time nor material permitted investigation of



TABLE L. - RANGE OF VARIATION IN MICRONESIAN CHAROPINAE, II.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER
<i>Jokajon</i>					
<i>callizonus</i>	32	127.6(99-153)	18.9(16.2-21.7)	0.93(0.79-1.06)	2.06(1.79-2.40)
<i>tumidulus</i>	142	106.1(74-148) <sup>1</sup> 53.6(39-69) <sup>2</sup>	14.61(10.35-22.9) <sup>1</sup> 8.13(5.80-10.62) <sup>2</sup>	1.30(1.10-1.65)	2.24(1.88-2.73)
<i>Palline</i>					
<i>micramyla</i>	3	138.0(130-146)	20.5(20.1-21.0)	1.02(0.97-1.06)	2.15(2.07-2.24)
<i>notera notera</i>	48	74.0(58-95)	11.63(9.37-15.66)	1.16(1.07-1.48)	2.02(1.89-2.37)
<i>notera palauana</i>	53	78.8(63-101)	11.01(8.71-12.87)	1.31(1.15-1.55)	2.26(2.04-2.50)
<i>notera gianda</i>	10	72.0(59-83)	9.44(7.92-10.57)	1.33(1.25-1.41)	2.43(2.34-2.50)
<i>biakensis</i>	1	90	12.90	1.23	2.22

1. Form with normal ribbing  
2. Form with widely spaced ribbing

	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	SPIRE ELEVATION
<i>calli.</i>	0.448(0.428-0.478)	4 1/2(4 1/8-5)	0.69(0.58-0.86)	2.98(2.79-3.27)	8.27(7-9)	0.06(0.03-0.07)
<i>tumid.</i>	0.581(0.528-0.642)	4 3/8-(4-5)	0.63(0.51-0.82)	3.56(2.98-4.18)	9.66(8-13)	0.11(0.05-0.20)
<i>micro.</i>	0.473(0.472-0.474)	4+	0.58(0.54-0.63)	3.67(3.55-3.79)	9	0 - 0.75
<i>n.not.</i>	0.572(0.537-0.625)	4+(3 3/4-4 5/8)	0.43(0.38-0.56)	4.75(4.24-5.26)	12.9(11-14)	0.11(0.07-0.13)
<i>n.pal.</i>	0.581(0.527-0.618)	4 1/8+(4-4 1/2)	0.57(0.49-0.66)	4.00(3.72-4.47)	13.3(11-15)	0.17(0.10-0.28)
<i>n.gia.</i>	0.549(0.526-0.573)	4 1/4-(4 1/8-4 3/8)	0.63(0.59-0.69)	3.89(3.57-4.16)	12.4(11-33)	0.13
<i>biake.</i>	0.556	3 7/8	0.49	4.50	14	0.12

	BODY WHORL WIDTH	SP/BW	PR	C	P
<i>calli.</i>	0.73(0.69-0.76)	0.075(0.048-0.089)	2	1	3+3
<i>tumid.</i>	0.83(0.72-0.95)	0.131(0.068-0.250)	2	1	3+5-6
<i>micro.</i>	0.73(0.72-0.74)	0.068	1	0	2
<i>n.not.</i>	0.75(0.71-0.81)	0.142(0.089-0.186)	3+0-1	0-1	5
<i>n.pal.</i>	0.82(0.76-0.94)	0.212(0.107-0.298)	2	0-1	3-4-5-6
<i>n.gia.</i>	0.87(0.84-0.92)	0.151(0.143-0.157)	3+0-1	0-1	3-4-5
<i>biake.</i>	0.76	0.152	1	0	0

this aspect, but it is an important problem for work with new and better preserved specimens.

The name *Jokajdon* refers to the occurrence of its two species in the Jokaj district of Ponape and their development of many complicated apertural barriers.

***Jokajdon tumidulus* (Möllendorff, 1900). Figure 92d-f.**

*Endodonta (Thaumatodon) callizona* var. *tumidula* Möllendorff, 1900, J. Malacol., 7 (5), p. 110—Mpomp and Naupilo, Ponape, Caroline Islands.

**Diagnosis.**—Shell very small, variable in size, diameter 1.88–2.73 mm. (mean 2.24 mm.), with 4–5 very tightly coiled whorls. Apex and early spire flat or barely protruding, lower spire descending slightly, body whorl much more rapidly, spire protrusion more than 1/6 body whorl width, H/D ratio 0.528–0.642 (mean 0.581). Apical sculpture of 8–13 (mean 9.66) fine, low spiral cords, whose interstices

are 2–3 times their width. Postnuclear sculpture highly variable, normally (52%) with high, narrow, crowded, slightly protractively sinuated radial ribs, 74–148 (mean 106.1) on the body whorl, whose interstices are less than twice their width; many examples (29%) with the ribs very widely spaced, 39–69 (mean 53.6) on the body whorl, whose interstices are 8–12 times their width, and often (19%) with major radial ribbing reduced to absent. Ribs/mm. 10.35–22.9 (mean 14.61) in normal form; 5.80–10.62 (mean 8.13) in widely spaced form. Microsculpture of fine radial riblets, 2–5 between each pair of major ribs in normally ribbed forms, 10–15 in widely spaced ribbed forms, with finer and more crowded spiral riblets, plus secondary spiral cords that are more prominent than the microradial riblets. Umbilicus open, broadly U-shaped, regularly decoiling, contained 2.98–4.18 times (mean 3.56) in the diameter, margins shouldered, walls of umbilicus distinctly flattened. Sutures deep, whorls strongly rounded above, compressed laterally with evenly rounded outer margin and strongly rounded basal margin. Aperture ovate, compressed laterally, inclined less than 10° from shell axis. Parietal barriers 2, extending posteriorly almost 1/4 whorl: upper a high, broadly expanded blade on posterior half, next quarter descending

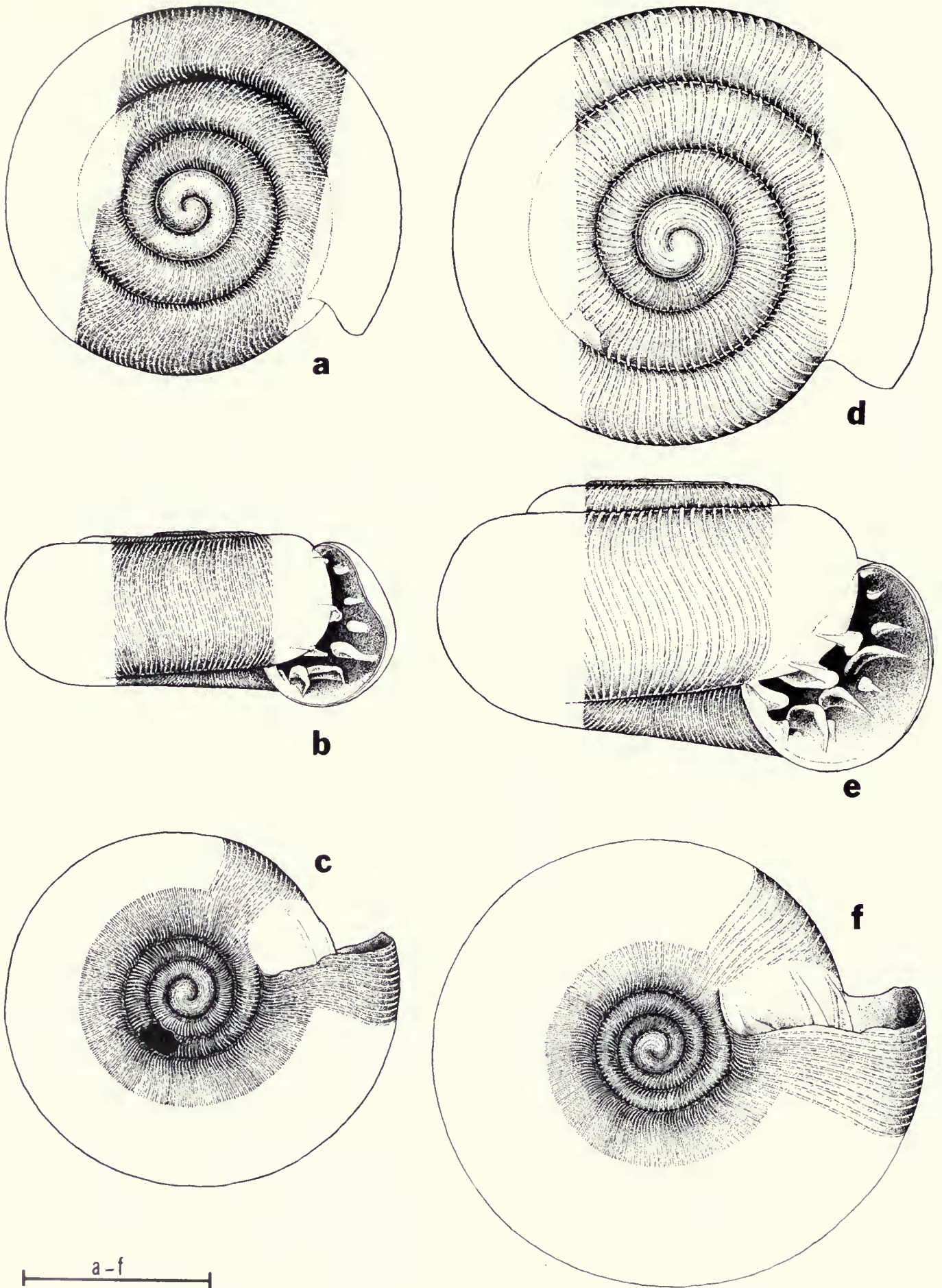


FIG. 92. a-c, *Jokajdon callizonus* (Möllendorff). Station 118, Ponape, Caroline Islands. BPBM 154161; d-f, *Jokajdon tumidulus* (Möllendorff). Station 146, Ponape, Caroline Islands. BPBM 157984. Scale line equals 1 mm. (MM).



rather sharply with a droplike accessory protrusion on lower side, anterior quarter low and broad, tapering to end point; 2nd much higher, sinuately twisted and crescentic over posterior  $\frac{3}{4}$ , anterior quarter a broad threadlike ridge tapering to a point anterior of upper parietal termination. Columellar wall with a single very high, crescentic barrier, very broadly expanded above and slightly sinuated posteriorly, anterior end twisted upward along columellar lip edge to terminate on lower parietal wall. Palatal barriers 3, very high, extending posteriorly more than  $\frac{1}{8}$  whorl, plus 6, rarely 5, accessory traces: lower at baso-columellar margin, very high and broadly expanded to a T-shape on posterior  $\frac{3}{4}$ , with anterior quarter weakly expanded above, descending abruptly to lip margin; 2nd moderately recessed, much lower, teardrop-shaped on posterior half, with gradual anterior descension of a thin lamellar blade; 3rd equal in height to 1st, sinuately twisted transversely upward, a thin blade with abrupt anterior descension, moderately recessed. Accessory traces, triangular knobs to very short lamellae, normally located between columellar and 1st palatal, 1st and 2nd palatals, 2nd and 3rd palatals, and 3 above 3rd palatal. Rarely one of the lower traces absent; upper traces usually short crescents, lower 3 highly variable in shape.

*Jokajdon tumidulus* (fig. 92d–f, table L) is much higher, has a narrower umbilicus, much thicker body whorl, and shows many differences in barrier structure from *J. callizonus* (fig. 92a–c). The large number of complexly expanded and twisted barriers are unique among Pacific Island endodontoid snails and prevent confusion with any other species.

*Description*.—Shell rather small, with slightly less than 4% very tightly coiled whorls. Apex and early spire flat, lower spire descending a little, body whorl descending sharply, H/D ratio 0.562. Apical whorls 1%, sculpture of 10 narrow, rather widely spaced spiral cords. Postnuclear whorls with prominent, moderately widely spaced, protractively sinuated radial ribs becoming quite crowded on last portion of body whorl. Microsculpture a lattice of very fine radial riblets, crossed by much finer and more crowded spiral riblets with a prominent secondary sculpture of moderately widely spaced spiral cords. Sutures deeply impressed, whorls strongly rounded above, greatly compressed laterally, with evenly rounded lateral and basal margin. Umbilicus U-shaped, slightly decoiling, contained 3.19 times in the diameter, slightly flattened internally with strongly rounded margins. Aperture ovate, compressed laterally, inclined less than 5° from the shell axis. Parietal barriers 2, extending slightly more than  $\frac{1}{8}$  whorl: upper moderately high, slightly twisted upward posteriorly with a broadly expanded, downwardly pointing, hatchet-shaped accessory plate on anterior half; lower quite high, crescentic, thick, rounded above, slightly sinuately twisted posteriorly with very gradual anterior descension, reaching past lip edge. Columellar barrier high, broadly rounded, twisting upward anteriorly, reaching columellar-parietal margin, sharply descending posteriorly. Major palatal barriers 3, with 6 accessory lamellae: lower palatal basal, a short, high, sinuately twisted blob greatly thickened in middle, only moderately recessed; middle palatal deeply recessed, much smaller in size, slightly thickened medially, crescent-shaped; upper palatal peripheral in position, hemispheric in shape, roundly expanded above, twisting laterally downward posteriorly, moderately recessed within aperture. Palatal traces located between columellar and 1st palatal, 1st and 2nd palatal, 2nd and 3rd palatal and 3, decreasing in size, above upper palatal. All traces short, ridgelike, or knoblike. Height of lectotype 1.42 mm., diameter 2.52 mm.

*Lectotype*.—Caroline Islands, Ponape. SMF 165702.

*Range*.—Ponape, Caroline Islands.

*Paratypes*.—SMF 165703, SMF 165756, BPBM 86247.

*Material*.—Ponape (16 specimens, BPBM 161092, DMW, FMNH 159359): one-quarter to three-quarters of the way up Mt. Tolotom (Stations 92, 93) at 800–1200 ft. elevation (29 specimens, BPBM 154082, BPBM

156680); Mt. Kuporujō (Station 121) at 500–900 ft. elevation (1 specimen, BPBM 154339); Wone, south side Mt. Tolotom (Stations 95, 98),  $\frac{1}{4}$  mile west at 900–1,000 ft. elevation (19 specimens, BPBM 156730–1, BPBM 156817–8); north of Sabalop (Station 123), south of Alokup-Najijo Mt. range at 60–150 m. elevation (4 specimens, BPBM 157318); above Mpomp (Station 125), 2 miles inland, at 75 ft. elevation (8 specimens, BPBM 157362–4); Toreairuku Mt., southwest side (Station 127)  $2\frac{1}{2}$  miles inland at 250–750 ft. elevation (1 specimen, BPBM 157420); Mt. Nanalaut, north slope (Stations 130, 132), at 400–1,900 ft. elevation (30 specimens, BPBM 157469, BPBM 157513–21); Palikir (Station 140), Mt. Tamantamansakir at 1,000–1,250 ft. elevation (6 specimens, BPBM 157866–7); Palikir (Station 139 = Station 138), Jokaj, 600–900 ft. elevation (1 specimen, BPBM 157800); Jokaj Island (Station 136), Rock, at 300–600 ft. elevation (1 specimen, BPBM 157704); Mt. Tolomain (Station 91), west side at 1,000–1,500 ft. elevation (4 specimens, BPBM 154005–6); back of Naupilo (Station 133) (11 specimens, BPBM 157566–7); summit of mountain above Station 145 (Station 146) at 860 ft. elevation (5 specimens, BPBM 157984–5).

*Remarks*.—Although Möllendorff considered that *Jokajdon tumidulus* was a variety of *J. callizonus*, the much thicker body whorl that descends rapidly and the more highly developed apertural barriers separate the two specifically (fig. 92b, e). At most localities on Ponape surveyed by Kondo, they did not occur together, but specimens of both species were found at Stations 91, 92, 93, and 95 on Roi Peak.

There is considerable variation in the sculpture of the shell in *J. tumidulus*, some specimens having the radial sculpture reduced to vague growth wrinkles. In other cases the radial ribs are very widely spaced (39–69 on the body whorl), and in most there is very strong, relatively crowded radial ribbing (79 to over 150 on the body whorl). There was some geographic basis to this variation, although wherever sufficient material was collected, generally two types were found together. The shells with greatly reduced radial sculpture were all found on the slopes of Mt. Tolotom, occurring alone at Station 92, but together with normally sculptured shells, although greatly in predominance, at Stations 93 and 95. The shells with very widely spaced but nevertheless prominent radial ribs were concentrated in north central Ponape, occurring with normally sculptured shells at Stations 132 and 140, but alone at Station 91. Specimens with only strong radial ribbing were found at Stations 98, 123, 125, 127, 130, 132, 133, 136, 139, and 146. The number of each sculptural type at the stations is summarized in Table LI.

No specimens at all transitional in sculptural type were seen. Because the specimens of all three types are identical in form and apertural barriers, I consider these to be minor genetic variations, probably in the process of spreading through the populations. The type

TABLE LI. — SCULPTURAL VARIATION IN  
JOKAJDON TUMIDULUS

Station	Type of sculpture		
	normal	reduced	widely spaced
91			4
92		2	
93	7	20	
95	1	13	
98	5		
121	1		
123	4		
125	8		
127	1		
130	3		
132	11		16
133	11		
136	1		
139	1		
140	3		3
146	5		
TOTALS	62	35	23

specimens all have normal sculpture. In addition to the sculptural variation discussed above, a few individuals from Station 146 on Jokaj Island, a single shell from Station 132 on Ponape, and specimens remaining in the type set are very large in size (table XLIX) and have the upper parietal barrier reduced in prominence. These probably represent gerontic individuals, and the variation is not of systematic importance.

Most specimens of *J. tumidulus* were monochrome in coloration, a light reddish yellow-brown, but a few showed traces of the lighter spiral zones that are characteristic of *J. callizonus*.

*Description of soft parts.*—No fully satisfactory dissections were obtained. Two rather squashed penes and poorly preserved apical genitalia were observed. Apical genitalia showed no differences from the structures seen in *Jokajdon callizonus*. Penis about 0.8–0.9 mm. long, cylindrical, tapering to middle and then to atrium, vas deferens and penial retractor as in *J. callizonus*. Interior of penis with weak longitudinal pilasters from apex to midpoint, a *Sinployeo*-type stimulatory pad developed just below midpoint. A muscle band inserts on penioviducal angle.

(Based on BPBM 156731, 2 whole examples.)

### *Jokajdon callizonus* (Möllendorff, 1900). Figures 92a–c, 93a–d.

*Endodonto* (*Thoumatodon*) *collizono* Möllendorff, 1900, J. Malacol., 7 (5), p. 110—Ponape, Caroline Islands.

*Diagnosis.*—Shell minute, diameter 1.79–2.40 mm. (mean 2.06 mm.), with 4½–5 extremely tightly coiled whorls. Apex and spire flat, or barely elevated, body whorl not descending more rapidly, spire protrusion about ¼ body whorl width, H/D ratio 0.428–0.478

(mean 0.448). Apical sculpture of 7–9 (mean 8.27) fine spiral cords, whose interstices are 3–5 times their width. Postnuclear sculpture of prominent, narrow, rounded, crowded, slightly protractively sinuated radial ribs, 99–153 (mean 127.6) on the body whorl, whose interstices are 1–2 times their width. Ribs/mm. 16.2–21.7 (mean 18.9). Microsculpture of fine radial riblets, 2–5 between each pair of major ribs, much finer and more crowded spiral riblets, with crowded, somewhat obscure secondary spiral cords equal in size to microradial riblets. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 2.79–3.27 times (mean 2.98) in the diameter, margins strongly rounded to weakly shouldered. Sutures deep, whorls strongly rounded to shouldered above, very strongly flattened laterally, with evenly rounded periphery and weakly compressed basal margin. Aperture subovate, strongly compressed laterally, inclined less than 10° from shell axis. Parietal barriers 2, extending posteriorly more than ¼ whorl almost to line of vision: upper very high and bladelike on posterior half, thin and sinuately twisted, posterior 8th twisted downward, abruptly descending about midpoint to threadlike anterior half reaching beyond lip margin; 2nd equal in height posteriorly to 1st, not sinuately twisted, with sharper descension near midpoint to threadlike anterior portion extending beyond end of upper. Columellar barrier a low, sometimes triangular knoblike ridge, deeply recessed within aperture, visible only by extreme tilting of aperture. Palatal barriers 3, moderately recessed, extending posteriorly more than ½ whorl, with 3 superior accessory traces: lower basal in position, very broadly expanded on posterior third and T-shaped, anterior half a thin, high blade with abrupt anterior descension to point midway across columellar callus; 2nd slightly lower than 1st, sinuately twisted outward and upward on posterior ¾, a lateral bifurcation on side of posterior half pointing inward and downward, crescentic, with gradual anterior descension, anterior end of main blade abruptly descending to point well behind anterior end of 1st; 3rd rather deeply recessed, shorter, posterior half grossly expanded into teardrop shape, with gradual anterior descension. Accessory traces very short, deeply recessed, broadly rounded, low crescentic to cordlike lamellae, evenly distributed between upper palatal and palatal-parietal margin, second usually slightly larger.

*Jokajdon callizonus* has a much narrower body whorl, (mean body whorl width 0.73 mm.), wider umbilicus, lower H/D ratio, and fewer palatal traces than does *J. tumidulus* (table L). In the latter, the body whorl descends rapidly and is much wider (mean body whorl width 0.83 mm.), the shell height is always larger and the umbilicus usually wider (fig. 92a–f). Other Micronesian species with numerous apertural barriers are much larger (*Semperdon kororensis* and *S. xyleborus*, fig. 98a–f) or have beaded barriers and usually angulated peripheries (*Aaadonta*, see Solem, 1976b, pp. 467–487).

*Description.*—Shell very small, with 4¼ very tightly coiled whorls. Apex and early spire flat, lower whorls descending slightly, H/D ratio 0.463. Apical whorls 1½, sculpture of 7 prominent, rather widely spaced spiral cords. Postnuclear whorls with slightly protractively sinuated, very crowded radial ribs, about 153 on the body whorl, whose interstices are less than twice their width. Microsculpture a lattice of fine microradial and spiral riblets with a secondary sculpture of much stronger, relatively closely set spiral cords. Sutures channeled, whorls evenly rounded above, strongly flattened laterally with gently rounded basal margin. Umbilicus broadly V-shaped, regularly decoiling, contained 3.09 times in the diameter. Color light reddish yellow-brown without darker flammulations or obvious spiral banding. Aperture ovate, strongly flattened laterally with strongly sinuated margin, inclined less than 10° from shell axis. Parietal barriers 2, extending posteriorly more than ¼ whorl, low and threadlike anteriorly becoming high and lamellate posteriorly. Columellar wall obscured by dried portion of animal. Major palatal barriers 3, with 3 accessory traces: lower palatal situated on basocolumellar margin, broadly expanded above, sinuately twisting downward onto basal lip; middle palatal moderately high, broadly expanded above, situated opposite lower parietal; upper palatal



peripheral in position, very broadly expanded above, somewhat sinuately twisted, moderately deeply recessed within aperture. Accessory palatals low, short, broad, deeply and equally recessed within aperture, located above upper palatal. A 4th palatal knob, very low and broad, located between lower 2 palatals. All major barriers minutely pustulose above. Height of lectotype 1.04 mm., diameter 2.24 mm.

**Lectotype.**—Caroline Islands, Ponape. Collected by Etscheid. SMF 165700.

**Range.**—Ponape, Caroline Islands.

**Paratypes.**—BPBM 86246, SMF 165701.

**Material.**—Ponape: Mt. Tolotom (Stations 92, 93), one-quarter to three-quarters of the way up at 800–1,200 ft. elevation (10 specimens, BPBM 9688, BPBM 156679); Metalanim to Nipit (Station 118), 450 ft. inland at 300–900 ft. elevation (14 specimens, BPBM 154161, BPBM 157282); west side Mt. Tolomain (Station 91) at 1,000–1,500 ft. elevation (1 specimen, BPBM 154007); Wone (Station 95), south side of Mt. Tolotom at 900 ft. elevation (1 specimen, BPBM 156732); Paishapal Hill (Station 113), Metalanim, at 650–700 ft. elevation (1 specimen, BPBM 157210).

**Remarks.**—Although specimens of *Jokajdon callizonus* and *J. tumidulus* were taken at Stations 91, 92, 93, and 95, no intergradation could be detected. The differences between them are substantial, and I consider that they represent valid species. A most unusual feature of *J. callizonus* is the spirally zoned color pattern seen in most examples. One or two light yellow spiral bands will interrupt the basic reddish brown color. These zones are highly variable in position and width. No attempt was made to analyze this variation. Much less size variation was found between local populations than in *J. tumidulus* (table XLIX).

**Description of soft parts.**—Foot and tail much shorter than shell diameter, tapering posteriorly. Pedal grooves and slime network typical. Head retracted in all studied material. Body color white with a faint yellow tinge, no darker markings. Mantle collar (MC) rather wide, edge thickened, no glandular extension onto pallial roof. Anus (A) opening slightly behind external ureteric pore (KX).

Pallial region (fig. 93a) extending apically for more than  $\frac{3}{4}$  whorl, quite narrow. Lung roof clear, no granulations. Kidney (K) bilobed, rectal arm about 1.51 mm. long, covering hindgut and extending halfway down parietal wall. Pericardial arm very short and narrow, scarcely longer than heart. Ureter (KD) without unusual features. Heart (H) parallel to hindgut, a little shorter than pericardial kidney arm. Principal pulmonary vein (HV) narrow, unbranched. Hindgut (HG) extending slightly apical of pallial cavity.

Ovotestis a single clump of 3 or 4 clavate acini above stomach apex, lying parallel to whorl sides and weakly iridescent. Hermaphroditic duct very slender, not convoluted. Albumen gland short, compact, acini small. Talon (fig. 93d, GT) with globular head. Prostate (fig. 93b, DG) with a few large acini. Uterus (UT) typically bipartite.

Vas deferens (VD) highly convoluted, entering laterally on head of penis with junction of retractor muscle (fig. 93c). Penial retractor (PR) long, inserting directly in head of penis-vas junction. Penis (P) short, cylindrically bitapered, about 0.3–0.4 mm. long, upper tapered area with a few weak pilasters, internal structure of median bulge not worked out in detail, but apparently with a thick muscular pad or pilaster, probably as in *J. tumidulus*. Atrium (Y) short, without unusual features.

Free oviduct (UV) quite short, tapering. Spermatheca (S) with large oval head, slender shaft at most weakly expanded before joining with free oviduct. Vagina (V) quite long, narrow, with internal pilasters. Free muscle system unusual in having a separate muscle

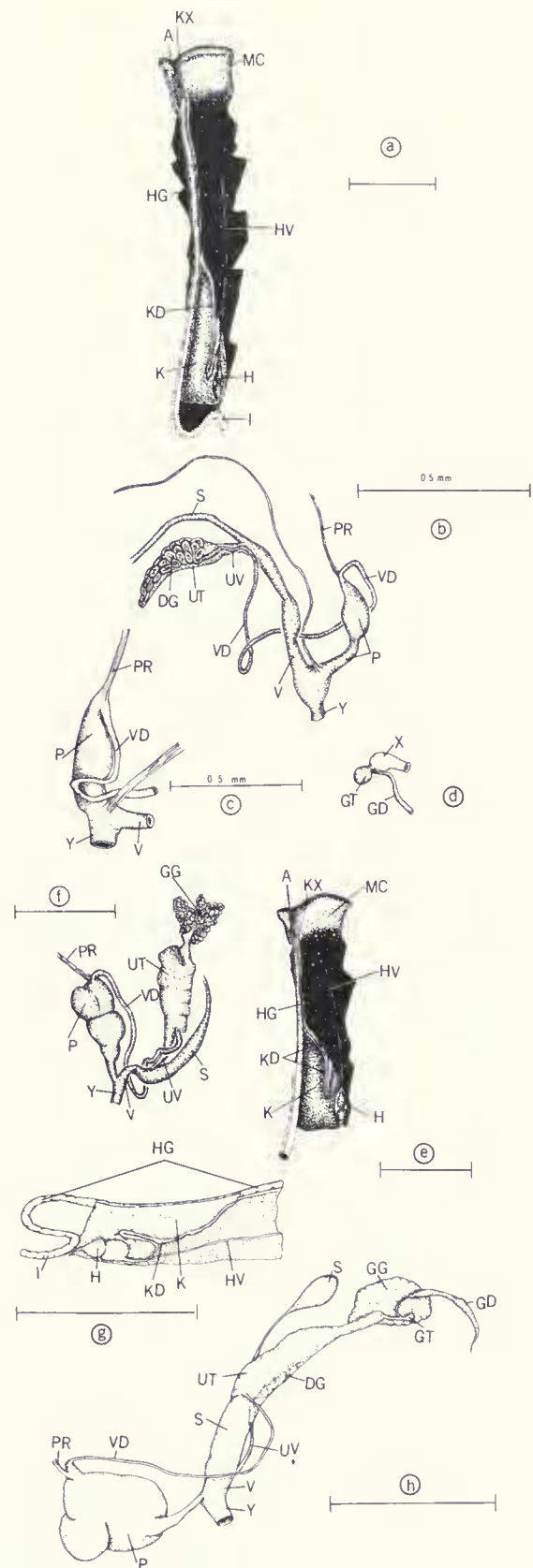


FIG. 93. Anatomy of *Jokajdon* and *Palline*: a–d, *Jokajdon callizonus* (Möllendorff). Sta. 118, Ponape. BPBM 154161. a, pallial region. b, genitalia. c, detail of penis-vas deferens junction. d, detail of talon-carrefour region; e–f, *Palline notera notera*, new species and subspecies. Station 201, Peleliu. BPBM 159946. e, pallial region. f, genitalia; g–h, *Palline micramyla*, new species. Station 137, Palikir, Ponape. Holotype. BPBM 157731; g, pallial region; h, genitalia. Scale lines equal 1 mm. (a–b, e–f, MO; c–d, JC & AS; g–h, PS).

band inserting on penioviducal angle. Right ommatophoral retractor passing through penioviducal angle.

(Based on BPBM 154161, 4 whole specimens.)

### Genus *Palline*, new genus

Shell smaller than average, with 3 $\frac{3}{4}$ –4 $\frac{1}{4}$  normally coiled whorls. Apex and spire slightly to moderately elevated, body whorl descending more rapidly. Apical sculpture of a variable number of prominent spiral cords. Postnuclear sculpture of narrow, moderately spaced to crowded, almost vertically sinuated radial ribs. Microsculpture of extremely fine radial and spiral riblets with prominent, rather widely spaced secondary spiral cording. Umbilicus rather broadly V-shaped to narrowly U-shaped, margins rounded. Whorls strongly rounded above and compressed laterally to strongly flattened laterally above rounded periphery, aperture inclined less than 10° from shell axis. Parietal barriers variable in number, from 3, short and high, to 1 or 2. Columellar wall with or without a low threadlike ridge. Palatal barriers usually 4–6, reduced to 2 in *micramyla*, absent in *biakensis*. Pallial region extending  $\frac{1}{2}$  whorl apically, kidney with rectal arm much longer than pericardial and extending over hindgut onto parietal wall, pericardial arm about 50% longer than heart and greatly reduced in size. Ototestis with two clumps of alveoli. Vas deferens passing through penial retractor muscle before latter inserts on head of penis. Penis of medium length, covered by a thin muscle sheath, head bulging with external constrictions indicating 3 internal zones: a lateral or upper zone with a tubular verge leading from vas deferens; an upper part to the side of the verge or shifted downward with 2 circular glandular pilasters; and a lower zone with thick circular or horseshoe-shaped pilaster tapering into narrowed shaft leading to atrium.

*Type species.*—*Palline notera notera*, new species and subspecies.

*Palline* (fig. 93e, g) agrees with *Jokajdon* (fig. 93a) in structure of the pallial region, although the degree of rectal kidney arm descension onto the parietal wall is greater in the latter genus. *Palikirus* has the kidney arms less disparate in size than in *Palline*, but the degree of crossing onto the parietal wall is about the same. The genitalia of *Palline* (fig. 93f, h) is unique among the Pacific Island Charopidae in the possession of a distinct tubular verge. Although *Kubaryiellus* (fig. 90g) has a modified pillow-like vergic papilla and the *Sinployea* structure is dominant in Polynesia, none of the remaining Micronesian genera have other than a simple pore from the vas deferens into the penis. Development of a true verge is common in New Zealand taxa, and the relatives of *Palline* may be found in the Southern Relict endodontoid taxa. The pair of concentric glandular pilasters and the thick horseshoe pilaster of *Palline* also are very different from the structures seen in other Micronesian genera. Passage of the vas deferens across the penis head and through the penial retractor muscle agrees with most of the Micronesian taxa.

Conchologically, *Palline* shows few unusual features. *Palline notera* (fig. 94a–f) from the Palau Islands has a very strong callus on the columellar and palatal walls that at times “buries” the smaller barriers. Otherwise it is a small species with quite prominent ribbing, a protruded spire, many spiral apical cords, a relatively narrow umbilicus, and slight lateral flattening of the whorls. *Palline micramyla* (fig. 95c–e) from Ponape has much finer and more crowded radial rib-

bing, a less protruded spire, fewer spiral apical cords, a slightly wider umbilicus, and the whorls are strongly flattened laterally above the periphery rather than on the outer margin. Both species agree in having a somewhat lower whorl count than the other toothed Micronesian species and in having the major ribbing almost vertically sinuated. *Palline biakensis* (fig. 96a–c) from Biak Island, West Irian, has only one parietal and no palatal barriers. Otherwise it falls within the range of variation for *P. notera notera*. Shell color is light yellow or reddish yellow-horn without conspicuous darker markings in all species, although some examples of *Palline notera gianda* show faint flammulations. Although the shell form of the Ponape species is much more similar to some of the other Caroline Island taxa, the anatomy clearly places it with *Palline notera*.

On the basis of initial conchological study, I had assumed that *Semperdon uncatus* was closely related. Discovery that it had such a very different penial structure was one of the more surprising aspects of this project. Shell differences from *Palline notera* are discussed below.

The name *Palline* is manufactured from the first three letters of Palau and the last four of Caroline to indicate that this genus is found in both areas.

### *Palline notera*, new species.

Populations on Babelthuap, Koror, and Peleliu agree in basic shell form and structure, but show minor differences in barrier size and number plus shell size and proportions. No anatomical differences were observed between the populations, and subspecific recognition has been given. The exact differences are outlined under the diagnosis of the three races—*Palline notera notera* from Peleliu, *Palline notera gianda* from Babelthuap, and *Palline notera palauana* from Koror.

Of the Micronesian species, only *Semperdon uncatus* (fig. 97a–c) is apt to be confused with *Palline notera*. At first inspection, shells of *S. uncatus* could be interpreted as gerontic individuals of the latter species. Reduction in apertural callus and barrier size in very large gerontic individuals is known for *Minidonta simulata*, Solem & Cooke (Solem, 1976b, p. 147, fig. 70d). Barrier position in *S. uncatus* agrees with *Palline notera*. The former lacks secondary spiral cording, averages a half whorl more, has fewer spiral cords on the apex, and has a totally different penial structure. The similarities are even greater than those between *Sinployea kusaieana* and *Trukcharopa trukana*, but the relationship is no closer.

Conchological differences between *Palline notera* and *P. micramyla* were outlined above under the generic discussion. Anatomical differences are few, with the shorter penis and downward shift of the thin-walled pocket the most obvious alteration. *Palline biakensis* is almost identical with *P. notera notera*, but is immediately recognizable by having only a single parietal and no palatal barriers.



***Palline notera notera*, new species and subspecies.  
Figures 93e–f, 94a–c.**

**Diagnosis.**—Shell very small, diameter 1.89–2.37 mm. (mean 2.02 mm.), with 3%–4% rather tightly coiled whorls. Apex and spire slightly and evenly elevated, body whorl descending more rapidly, spire protrusion about  $\frac{1}{2}$  body whorl width, H/D ratio 0.537–0.625 (mean 0.572). Apical sculpture of 11–14 (mean 12.9) prominent spiral cords whose interstices are about 2–3 times their width. Postnuclear sculpture of high, rounded, prominent, almost vertically sinuated radial ribs, 58–95 (mean 74.0) on the body whorl, whose interstices are 2–5 times their width. Ribs/mm. 9.37–15.66 (mean 11.63). Microsculpture of barely visible radial riblets, 5–12 between each pair of major ribs, equally fine spiral riblets, plus much more prominent secondary spiral cords, whose interstices are 3–6 times their width. Umbilicus rather narrow, U-shaped, slightly and regularly decoiling, contained 4.24–5.26 (mean 4.75) times in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally, with evenly rounded outer margin. Aperture ovate, compressed laterally, inclined about  $5^\circ$  from shell axis. Parietal barriers 3, short, high, extending posteriorly about  $\frac{1}{2}$  whorl, occasionally with an accessory trace: upper with abrupt descension over posterior 8th, very much higher and crescentic over next quarter, with gradual anterior descension becoming rapid over anterior quarter, posterior elevated portion slightly twisted downward; 2nd equal in height and posterior descension to 1st, crescentic until  $\frac{3}{4}$  point, with gradual anterior descension on last 3rd to point beyond termination of upper parietal; 3rd greatly reduced in height, a raised threadlike ridge with more elevated crescentic portion on posterior 3rd, equal in length to 2nd parietal. Columellar wall with single threadlike ridge, lying parallel to plane of coiling, reaching to top of very thick columellar callus, often (2 of 13) covered by callus, which extends on palatal wall almost to periphery. Palatal barriers 5, short, slightly recessed: lower basal in position, very high and crescentic, slightly expanded above, with abrupt sinuately twisted descension to lip edge, more gradual descension posteriorly; 2nd and 3rd less than  $\frac{3}{4}$  height of 1st, crescentic, moderately expanded above, slightly recessed, with much more gradual anterior descension; 4th higher than 3rd, lower than 1st, crescentic, expanded above with rather sharp anterior descension, slightly subperipheral; 5th slightly lower than 3rd, but otherwise matching it in structure, located above level of upper parietal, moderately recessed.

*Palline notera notera* (fig. 94a–c) is smaller and has a much narrower umbilicus than either *P. notera gianda* (fig. 95a–b), which usually has only four palatals and lacks the columellar, or *P. notera palauana* (fig. 94d–f), which has only two parietals, usually no columellar, and only four palatals. *Palline biakensis* (fig. 96a–c) has only one weak parietal and no palatal barriers, otherwise it is nearly identical to *P. notera notera*.

**Description.**—Shell very small, with 4% moderately tightly coiled whorls. Apex and spire almost flat, body whorl descending slightly, H/D ratio 0.565. Apical whorls 1%, sculpture of 11 prominent spiral cords. Postnuclear whorls with prominent, high, rounded, vertically sinuated radial ribs, 84 on the body whorl, whose interstices are 3–4 times their width. Microsculpture of fine, crowded radial riblets, crossing very faint crowded spiral ribs with a secondary sculpture of prominent, rather widely spaced, spiral cords. Sutures deeply impressed, whorls strongly rounded above with slightly flattened basal margin, compressed laterally. Color light yellow-horn, without darker markings. Umbilicus narrowly U-shaped, slightly and regularly decoiling, contained 5.24 times in the diameter. Aperture ovate, inclined less than  $5^\circ$  from the shell axis with moderately prominent internal callus. Parietal barriers 3, extending posteriorly less than  $\frac{1}{2}$  whorl; upper a thin, high barrier with gradual anterior descension over anterior half, slightly expanded above on posterior 8th and twisted downward; 2nd parietal higher, elevated and expanded on posterior half, with more gradual anterior

descension; 3rd parietal much lower, a threadlike ridge. Columellar wall with a low, broad swelling reaching top of heavy callus. Palatal barriers 5, extending about  $\frac{1}{6}$  of a whorl: 1st and 4th relatively high, slightly expanded above, crescent-shaped; 2nd, 3rd, and 5th much lower, narrower, shorter, more deeply recessed. Height of holotype 1.22 mm., diameter 2.16 mm.

**Holotype.**—Palau Islands: Peleliu, Station 201, short distance to north of phosphate mine at 35–200 ft. elevation. Collected by Yoshio Kondo and natives on April 29, 1936. BPBM 159946.

**Range.**—Peleliu, Palau Islands.

**Paratypes.**—Peleliu: short distance to north of phosphate mine (Station 201) at 35–200 ft. elevation (41 specimens, BPBM 159944–9); Omurbrogol Mt., Asias Village (Station 182),  $\frac{1}{2}$ – $\frac{3}{4}$  mile inland at 300–400 ft. elevation (4 specimens, BPBM 159432–3); on hill east of Station 176 (Station 184), 100 yd. inland at 200 ft. elevation (1 specimen, BPBM 159517); 300–400 yd. north of Station 201 (Station 203) on hillside (1 specimen, BPBM 159994).

**Remarks.**—One specimen had an accessory trace between the second and third parietals, but otherwise there was little variation in the apertural barriers. Apparently this species is widely distributed on Peleliu.

It was not possible to illustrate the interior of the penis. The verge has only about one-quarter of its length as a free tip with central pore and wrinkled muscular sides, whereas the upper three-quarters is a thinner-walled, slightly expanded chamber that may function as an epiphallus in forming a sperm packet. Vas deferens enters the apex of this chamber after passing through the penial retractor muscle. Lateral to the verge is a very thin-walled, bulging pocket with two concentric rings of glandular pilasters, with a constricted opening to the lower chamber with its very wide and solid pilaster.

**Description of soft parts.**—Foot and tail much less than shell diameter, shape typical. Sole, pedal grooves, and slime network without unusual features. Body color yellow-white, without darker markings. Anus (A) opening inside pneumostomal pore, anterior of external ureteric pore (KX).

Pallial region (fig. 93e) extending  $\frac{1}{2}$  whorl apically. Lung roof without granulations. Kidney (K) short and broad, 1.0–1.1 mm. long, rectal lobe much longer than pericardial, partly extending onto parietal wall. Ureter (KD) with primary and first part of secondary sections compacted between arms of kidney, latter portion of secondary ureter slightly tapered to anterior. Heart (H) shorter than pericardial arm of kidney, lying parallel to hindgut. Principal pulmonary vein (HV) unbranched. Hindgut (HG) without unusual features.

Ovotestis with 2 clumps, 1 above the other, of 3–4, iridescent white, long alveoli imbedded in digestive gland above stomach apex. Hermaphroditic duct not observed in adult condition. Albumen gland (fig. 93f, GG) with relatively large acini. Talon not observed. Prostate (DG) and uterus (UT) without unusual features.

Vas deferens (VD) entering penis head after passing through penial retractor muscle in transversing penis head. Penial retractor (PR) short, arising from diaphragm, inserting onto penis head after enfolding vas deferens. Penis (P) with elongated bulging head of about 0.7–0.8 mm. length followed by a much shorter, tubular shaft. Upper portion covered by a thin muscle sheath, internally very complex, apparently with a verge occupying one side of upper bulge, other half with 2 concentric circular pilasters with exceedingly thin

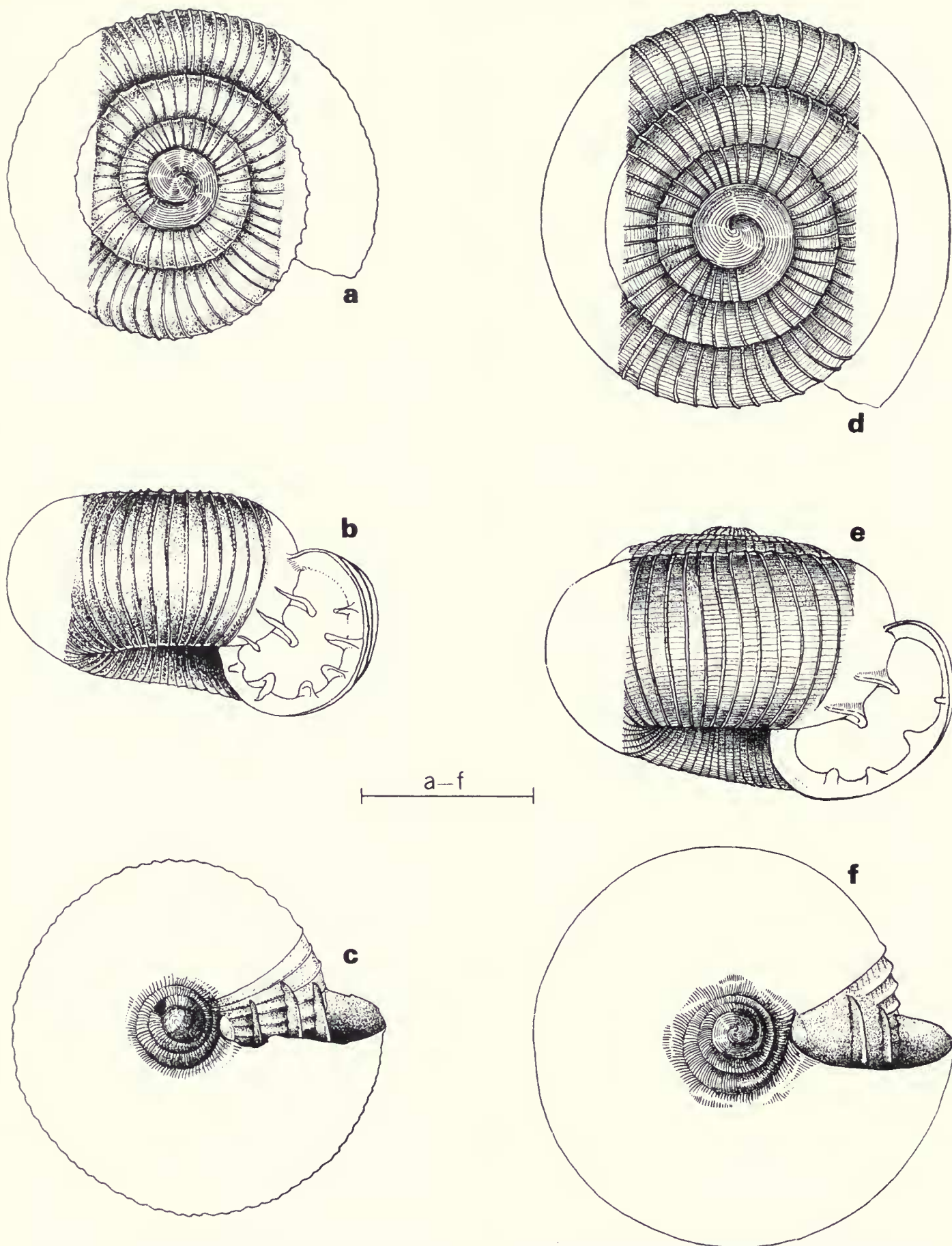


FIG. 94. a-c, *Palline notera notera*, new species and subspecies. Station 201, Peleliu, Palau Islands. Holotype. BPBM 159946; d-f, *Palline notera palauana*, new subspecies. Station 220, Ittabagamin, Koror, Palau Islands. Holotype. BPBM 159046. Scale line equals 1 mm. (SG).



walls, then a thick pilaster occupying lower bulge of penis head that is horseshoe-shaped with ends tapering toward atrium. Atrium (Y) a narrow tube.

Free oviduct (UV) very slender, tapering from uterus. Spermatheca (S) with elongately oval head, lower half of shaft grossly expanded. Vagina (V) rather long, equal in diameter to lower part of penis. Free muscle and digestive systems without unusual features.

(Based on BPBM 159946, 2 whole subadults and several fragmentary adults.)

***Palline notera palauana*, new subspecies. Figure 94d-f.**

**Diagnosis.**—Shell small, diameter 2.04–2.50 mm. (mean 2.26 mm.), with 4–4½ tightly coiled whorls. Apex and spire slightly to strongly elevated, body whorl descending more rapidly, spire protrusion usually more than ½ body whorl width, H/D ratio 0.527–0.618 (mean 0.581). Apical sculpture of 11–15 (mean 13.3) prominent spiral cords, whose interstices are less than twice their width. Postnuclear whorls with high, prominent, rounded, almost vertically sinuated radial ribs, 63–101 (mean 78.8) on the body whorl, whose interstices are 3–5 times their width. Ribs/mm. 8.71–12.87 (mean 11.01). Microsculpture of very fine radial riblets, 6–12 between each pair of major ribs, crossed by barely visible spiral riblets, with a secondary sculpture of much more prominent, rather widely spaced spiral cording. Umbilicus rather widely open, U-shaped, slightly and regularly decoiling, contained 3.72–4.47 times (mean 4.00) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above and on basal margin, compressed laterally, outer margin evenly rounded. Aperture compressedly ovate, inclined about 5° from shell axis. Parietal barriers 2, extending posteriorly more than ½ whorl, occasionally with a threadlike trace occupying position of 3rd parietal in nominate race: upper high, bladelike, slightly more elevated and expanded on posterior quarter, with gradual descension over anterior half; 2nd usually slightly reduced in height, more broadly expanded above on posterior half, with gradual descension to point beyond end of upper or no descension until anterior quarter. Columellar wall normally without barriers, occasionally with a weak threadlike trace. Palatal wall normally (75%) with 4 rather short, low, crescentic barriers, frequently either 3, 5, or 6: lower basal in position, low, broadly rounded, with rather abrupt descension across callus to lip margin; 2nd and 3rd slightly lower, a little more recessed, with more gradual anterior descension; 4th a moderately recessed, supraparapheral, threadlike trace. Callus very broad, extending from columellar wall to parietal-palatal margin, only slightly decreasing in thickness.

*Palline notera palauana* has a relatively protruding spire, only two parietals, and a wider umbilicus than the nominate race with its three parietals and relatively narrow umbilicus. *Palline notera gianda* is larger, has three parietals, and the spire protrusion is less (table L).

**Description.**—Shell small, with 4½ tightly coiled whorls. Apex and spire moderately and evenly elevated, last whorl descending more rapidly, spire protrusion almost ½ body whorl width, H/D ratio 0.618. Embryonic whorls 1½, sculpture of 15 prominent, closely spaced spiral cords. Postnuclear whorls with prominent, high, vertically sinuated radial ribs, 101 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets with traces of extremely fine spiral riblets and a secondary sculpture of relatively prominent, widely spaced spiral cords. Sutures deep, whorls strongly rounded above, compressed laterally. Umbilicus U-shaped, regularly decoiling, contained 4.00 times in the diameter, margins rounded. Color light yellow-horn without darker flammulations. Aperture ovate, compressed laterally, inclined about 5° from shell axis. Parietal barriers 2, extending posteriorly about ½ whorl, upper less expanded, slightly reduced in height, with sharper anterior descension. Palatal barriers 4, low and crescentic, extending less than ½ whorl: 1st and 3rd palatals prominent, broadly rounded short ridges; 2nd and 4th markedly reduced in prominence; 4th a

threadlike ridge. All palatal barriers situated on a heavy apertural callus. Height of holotype 1.55 mm., diameter 2.50 mm.

**Holotype.**—Palau Islands: Koror, Islet XV, Station 220, Ittabagamin, at 15–20 ft. elevation. Collected under stones and on dead leaves by Yoshio Kondo on May 11, 1936. BPBM 159046.

**Range.**—Koror and satellite islets, Palau Islands.

**Paratypes.**—Koror: Islet XV (Station 220), Ittabagamin, at 15–20 ft. elevation (4 specimens, BPBM 159046–7); Komakan (Station 219), south below Station 218, 50–75 yd. inland at 75 ft. elevation (1 specimen, BPBM 158783); northeast side, western neck of island, Islet XXIX (Station 212), 10 yd. inland at 30–100 ft. elevation (2 specimens, BPBM 159107); in forest on limestone (1 specimen, BPBM 193146, collected by E. V. Hosaka on July 20, 1946); in abandoned quarry, Nerubodoru, near lagoon shore, northeast part of island, 20–25 ft. elevation (44 specimens, USMN, FMNH 159395, BPBM 212387).

**Remarks.**—Variation in the degree of spire protrusion was much more marked than in most species. This was caused by two individuals having relatively low spires (SP/BWW 0.107 and 0.122) and five having high spires (SP/BWW 0.239, 0.250, 0.250, 0.292, 0.298). The standard error of the mean for 10 measured examples was 0.082, whereas for seven examples of *Palline notera notera* it was 0.013, and for 18 specimens of *Semperdon xyleborus* it was 0.010. *Semperdon uncatus*, with only four examples measured, had a standard error of the mean of 0.084 and showed a range of variation equal to that seen in *P. notera palauana*. The greater variation in these two taxa is not a function of age bias, but a real difference in spire elevation. Further study will be required to interpret these changes.

Specimens were collected both on Koror and on two of the satellite islets. Those from Islet XV (Station 220) are appreciably larger than those from Nerubodoru on Koror (table LII), but the latter are dead specimens of uncertain age. Many had been damaged during cleaning, and their smaller mean size probably has no significance.

***Palline notera gianda*, new subspecies. Figure 95a–b.**

**Diagnosis.**—Shell small, diameter 2.34–2.50 mm. (mean 2.43 mm.), with 4½–4¾ rather tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending more rapidly, spire protrusion more than ½ body whorl width, H/D ratio 0.526–0.573 (mean 0.549). Apical sculpture of 11–13 (mean 12.4) prominent spiral cords, whose interstices are 2–4 times their width. Postnuclear sculpture of prominent, high, rounded, almost vertically sinuated radial ribs, 59–83 (mean 72.0) on the body whorl, whose interstices are 2–5 times their width. Ribs/mm. 7.92–10.57 (mean 9.44). Microsculpture of very fine radial riblets, 5–10 between each pair of major ribs, barely visible spiral riblets and much more prominent, relatively crowded secondary spiral cords. Umbilicus rather widely open, U-shaped, moderately and regularly decoiling, contained 3.57–4.16 (mean 3.89) times in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above and on basal margins, compressed laterally, outer margin evenly rounded. Aperture ovate, compressed laterally, inclined about 5° from shell axis. Parietal barriers 3, extending posteriorly more than ½ whorl, sometimes with an accessory trace: upper high and bladelike, abruptly descending on

TABLE LII. - LOCAL VARIATION IN PALLINE.

NAME	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER
<u>notera palauana</u>					
Koror, Sta. 220 BPBM 159046-7	3	92.0±6.25 (80-101)	11.84±0.833 (10.19-12.87)	1.41±0.072 (1.32-1.56)	2.49±0.022 (2.45-2.52)
Nerubodoru, Koror BPBM 212387	10	74.3±2.19 (63-84)	10.74±0.362 (8.71-11.93)	1.28±0.022 (1.15-1.38)	2.19±0.028 (2.04-2.30)
<u>notera notera</u>					
Sta. 201 BPBM 159945,-7,-9	9	72.1±3.18 (58-84)	11.38±0.464 (9.37-13.57)	1.15±0.018 (1.07-1.22)	2.02±0.025 (1.94-2.15)
<u>notera gianda</u>					
Sta. 15 BPBM 160526-8	6	72.0±5.17 (59-83)	7.61±0.093 (7.35-7.85)	1.34±0.022 (1.26-1.42)	2.45±0.026 (2.35-2.52)
	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>n. pal</u>					
Sta. 220	0.566±0.0271 (0.527-0.618)	4 1/4(4-4 1/2)	0.64±0.011 (0.63-0.66)	3.90±0.058 (3.80-4.00)	14.33±0.664 (13-15)
Nerub.	0.586±0.0063 (0.561-0.618)	4 1/8(4-4 1/4)	0.55±0.011 (0.49-0.59)	4.04±0.074 (3.72-4.47)	12.83±0.477 (11-14)
<u>n. not</u>					
Sta. 201	0.570±0.0063 (0.541-0.600)	4+(3 3/4-4 1/4)	0.43±0.006 (0.41-0.46)	4.75±0.083 (4.37-5.24)	12.56±0.377 (11-14)
<u>n. gia.</u>					
Sta. 15	0.549±0.0078 (0.526-0.573)	4 1/4-(4 1/8-4 3/8)	0.63±0.161 (0.59-0.69)	3.89±0.082 (3.57-4.16)	12.40±0.398 (11-13)

posterior 8th, next quarter weakly elevated and moderately expanded, with gradual anterior descension; 2nd equal in height, elevated and expanded on posterior 3rd after initial abrupt descension, with more gradual anterior descension to point anterior of upper parietal; 3rd a very short, deeply recessed, threadlike ridge, sometimes with posterior half weakly elevated. Columellar wall normally without barriers, often (16%) with a weak threadlike ridge on top of heavy callus. Palatal barriers normally 4, often 3 (16%) or 5 (16%), slightly recessed, extending posteriorly  $\frac{1}{16}$ - $\frac{1}{8}$  whorl; lower basal in position, flatly crescentic, with sharp anterior descension across callus almost to lip edge; 2nd slightly lower, a little more recessed, with more gradual anterior descension; 3rd slightly subperipheral, pointing between upper 2 parietals, variable in height and width, more deeply recessed, equivalent to 4th palatal in nominate race; usually a threadlike lump located above 3rd palatal (equivalent to 5th in nominate race), often lacking; often a very faint threadlike trace present between 2nd and 3rd palatals.

*Palline notera gianda* is larger and much more widely umbilicated than the nominate race (table L). *Palline notera palauana* has a more strongly protruded spire and lacks the 3rd parietal.

*Description.*—Shell small, with  $\frac{4}{4}$  tightly coiled whorls. Apex flat, spire descending moderately, last whorl descending rapidly, H/D ratio 0.547. Apical whorls  $1\frac{1}{2}$ , sculpture of 13 relatively prominent spiral cords. Postnuclear whorls with prominent, high, rounded, nearly vertically sinuated radial ribs, 78 on the body whorl, whose interstices are 2-4 times their width. Microsculpture of fine radial riblets, 6-15 between each pair of major ribs, with traces of very fine crowded spiral riblets and a secondary sculpture of quite prominent, rather widely spaced spiral cords. Sutures deep, whorls strongly

rounded above, compressed laterally. Umbilicus broadly U-shaped, regularly decoiling, contained 4.16 times in the diameter, margins strongly rounded. Color light yellow-horn with vague reddish flammulations. Aperture ovate, almost parallel to the shell axis. Parietal barriers 3, extending posteriorly more than  $\frac{1}{8}$  whorl; upper a high, thin lamella, weakly expanded on posterior quarter, gradually descending until anterior 8th; 2nd lower, more broadly rounded above with very gradual anterior descension to point anterior to termination of 1st; lower a vague, threadlike ridge. Columellar wall without barriers, but with a heavy callus. Palatal wall with 3 barriers: lower moderately high, basal, extending less than  $\frac{1}{8}$  of a whorl; 2nd and 3rd progressively reduced in height and length. Height of holotype 1.35 mm., diameter 2.47 mm.

*Holotype.*—Palau Islands: Babelthuap, Station 15, Adelulu Hill, Airai-Mura, 30 m. inland at 20-40 m. elevation. Collected by S. Ito and natives on April 21, 1936. BPBM 160526.

*Range.*—Babelthuap, Palau Islands.

*Paratypes.*—Babelthuap: Adelulu Hill (Station 15), Airai-Mura, 30 m. inland at 20-40 m. elevation (9 specimens, BPBM 160526-8, BPBM 160532).

*Remarks.*—The larger size and wider umbilicus (table L) easily separate *Palline notera gianda* from the nominate race. The Koror Island *Palline notera palauana* is extremely close to *gianda*, but differs in having only two parietals and the palatal barriers more strongly developed. Only one station was made



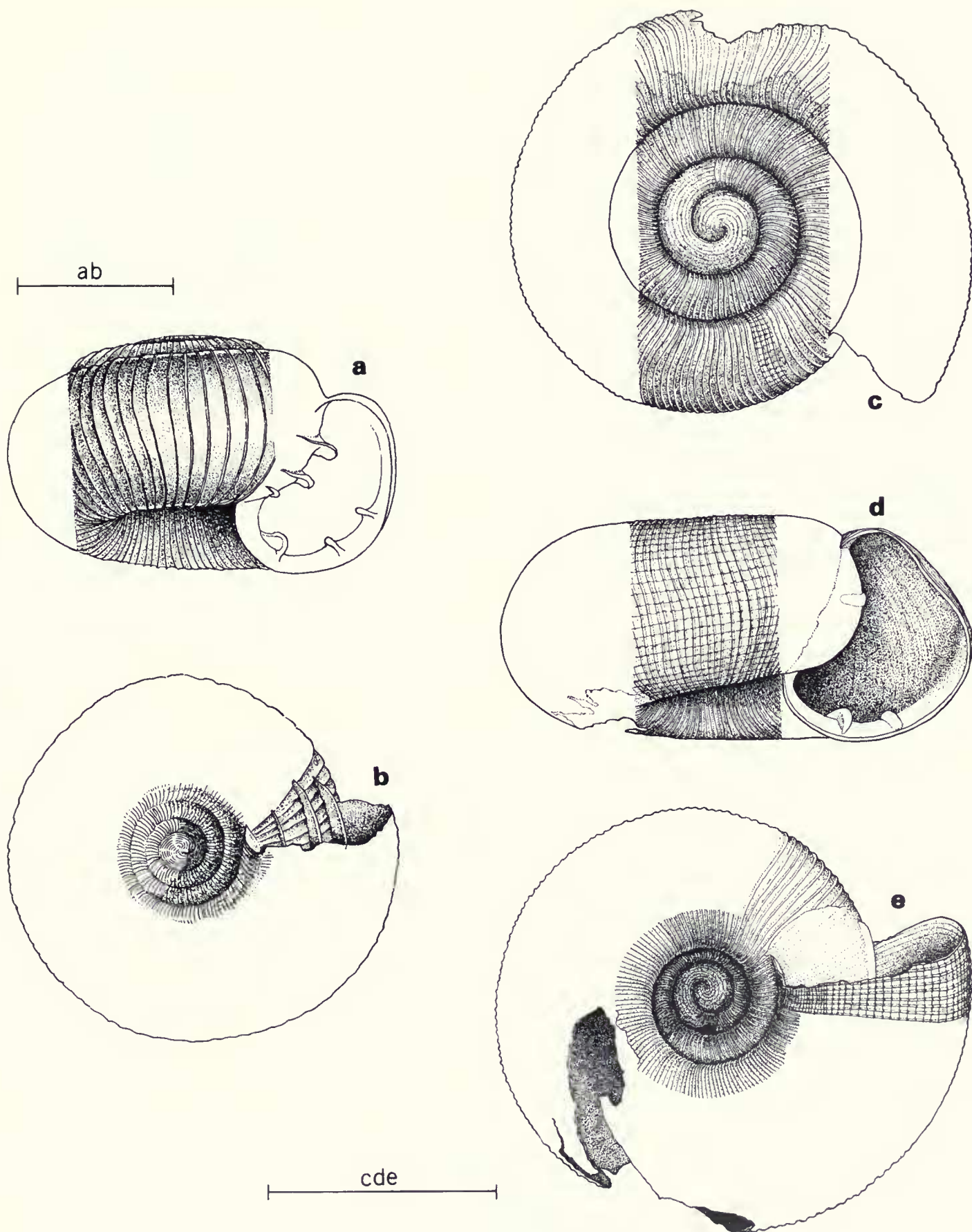


FIG. 95. **a-b**, *Palline notera gianda*, new subspecies. Station 15, Babelthuap, Palau Islands. Holotype. BPBM 160526; **c-e**, *Palline micramyla*, new species. Station 137, Palikir, Ponape, Caroline Islands. Holotype. BPBM 157731. Scale lines equal 1 mm. (*a-b*, SG; *c-e*, MM).

on Babelthuap so that the extent of distribution remains uncertain.

The name "*gianda*" is taken from the Hindustani term for the Asiatic rhinoceros. It refers to the comparatively large size of this race, and was the last new specific level name to be selected during this project.

***Palline biakensis*, new species. Figure 96a-c.**

**Diagnosis.**—A species very similar to the Palau Island *Palline notera*, but differing in having only a single parietal barrier and showing an unusual channeling of the suture.

**Description.**—Shell very small, with  $3\frac{3}{4}$  tightly coiled whorls. Apex and spire moderately and evenly elevated, body whorl descending much more rapidly, spire protrusion slightly more than  $\frac{1}{2}$  body whorl width, H/D ratio 0.556. Apical whorls  $1\frac{1}{2}$ , sculpture of 14 prominent spiral cords, whose interstices are less than twice their width. Postnuclear whorls with prominent, broadly rounded, slightly protractively sinuated radial ribs, 90 on the body whorl, whose interstices are 2–4 times their width. Ribs/mm. 12.90. Microsculpture of fine radial riblets, 4–9 between each pair of major ribs, crossed by much finer and more crowded spiral riblets, with prominent, rather widely spaced secondary spiral cording. Sutures deeply impressed, curled under and channeled at least on last half of body whorl, whorls strongly rounded above and on basal margin, slightly compressed laterally. Color light reddish yellow, without darker markings. Umbilicus rather narrow, U-shaped, regularly decoiling, contained 4.50 times in the diameter, margins rounded. Aperture ovate, slightly compressed laterally, inclined about  $15^\circ$  from shell axis. Parietal wall with single medial, rounded ridgelike barrier, extending posteriorly about  $\frac{3}{4}$  of a whorl. Columellar and lower palatal walls with prominent, gradually descending callus. Height of holotype 1.23 mm., diameter 2.22 mm.

**Holotype.**—West Irian: Biak, Hospitaalgrot (Hospital Cave), near Parai Camp. Collected March 20, 1952, during the Nieuw Guinea Expedition. RNHL.

**Range.**—Biak, West Irian.

**Remarks.**—Only the one specimen was collected. It agrees with *Palline notera notera* in every feature except barriers and the peculiar curled channeling of the sutures, which may be an individual abnormality.

***Palline micramyla*, new species. Figures 93g-h, 95c-e.**

**Diagnosis.**—Shell minute, diameter 2.07–2.24 mm. (mean 2.15 mm.), with  $3\frac{3}{4}$ –4 tightly coiled whorls. Apex and spire flat, last part of body whorl descending moderately, spire protrusion less than  $\frac{1}{4}$  body whorl width, H/D ratio 0.472–0.474 (mean 0.473). Apical whorls with 9 prominent, narrow, rather widely spaced spiral cords whose interstices are 3–5 times their width. Postnuclear whorls with narrow, crowded, sharply defined, almost vertically sinuated radial ribs, 130–146 (mean 138.0) on the body whorl, whose interstices are less than 2 to almost 4 times their width. Ribs/mm. 20.09–20.95 (mean 20.52). Microsculpture of extremely fine radial and spiral riblets barely visible under  $96\times$  magnification, probably 3–5 microradials between each pair of major ribs, plus quite prominent, widely spaced, secondary spiral cords, whose interstices are almost equal to the major rib spacing. Umbilicus broadly U-shaped, last whorl decoiling more rapidly, contained 3.55–3.79 times (mean 3.67) in the diameter, margins slightly shouldered. Sutures deep, whorls strongly rounded above and on baso-columellar margin, strongly flattened laterally above rounded periphery and on basal margin. Aperture ovate, compressed laterally, inclined about  $10^\circ$  from shell axis. Parietal wall with single supramedial, very low, threadlike barrier, extending posteriorly slightly more than  $\frac{1}{4}$  whorl, anterior end beyond lip edge. Columellar wall without barriers. Palatal barriers 2, basal in position, very short and low, almost reaching lip

margin: lower crescentic, broadly rounded, almost as wide as high; 2nd an oval tubercle, much lower and shorter, very slightly recessed from lip edge, also on basal lip.

*Palline micramyla* looks like a miniature *Trukcharopa trukana* (fig. 63d-f) with more flattened whorls and weak apertural barriers. *Roimontis tolotomensis* is much larger, has a deeply depressed apex and spire, two parietals, and less than 75 major radial ribs on the body whorl (fig. 91a-c).

**Description.**—Shell minute, with slightly more than 4 tightly coiled whorls. Apex and spire flat, last whorl descending slightly, H/D ratio 0.472. Apical whorls  $1\frac{1}{2}$ , sculpture of 9 narrow prominent spiral cords. Postnuclear whorls with crowded, rounded, protractively sinuated radial ribs, 130 on the body whorl, whose interstices are about twice their width. Microsculpture of greatly reduced microradials and microspirals with narrow, relatively prominent, widely spaced spiral cords. Sutures deep, whorls evenly rounded above, strongly flattened laterally above rounded periphery and less flattened on basal margin. Umbilicus U-shaped, last whorl decoiling more rapidly, contained 3.79 times in the diameter. Color a uniform light yellow-horn. Aperture ovate, somewhat flattened laterally, inclined about  $10^\circ$  from shell axis. Parietal wall with short, very low, threadlike barrier, extending posteriorly  $\frac{1}{4}$  whorl. Basal margin of lip with 2 short, ridgelike barriers located near margin, lower one more prominent. Height of holotype 0.97 mm., diameter 2.07 mm.

**Holotype.**—Caroline Islands: Ponape, Station 137, Palikir, a little more than  $\frac{1}{4}$  mile south of school at 450 ft. elevation. Collected on dead leaves by Yoshio Kondo and S. Ito on March 13, 1936. BPBM 157731.

**Range.**—Northern part of Ponape, Caroline Islands.

**Paratypes.**—Ponape: Not Point (Station 142) Peninsula, 10 yd. inland at 4 ft. elevation (2 specimens, BPBM 157926).

**Remarks.**—Only three specimens of the quite distinctive species were obtained. A live subadult from Station 137 near Palikir has been chosen as holotype. Two dead shells from Station 142 at Not Point were quite worn. In one the 2nd palatal was almost worn off, and the palatal wall was broken in the other. Secondary spiral cording is very prominent, clearly beading the major ribs upon crossing them, whereas the normal microsculpture can only be seen in strong lateral lighting under high magnification. Shell sculpture, size, and coiling pattern are quite different from *Roimontis tolotomensis*, despite the great similarity in general form.

**Description of soft parts.**—Body completely retracted within shell, tissues soft and poorly preserved. Foot and tail slender, tapering slightly posteriorly, pedal grooves typical, no caudal horn or foss.

Body color yellow-white, no darker markings. Eyespots black.

Mantle collar narrow, edge rounded, no conspicuous lobes developed, torn off in dissecting. Lung roof clear, without speckling. Kidney (fig. 93g, K) proportionately narrower than in *Palline notera*, partly deflected below hindgut (HG) and onto parietal wall, length of rectal lobe about 0.95 mm. Pericardial lobe much shorter, about  $1\frac{1}{2}$  times length of heart. Ureter (KD) tightly compacted between lobes of kidney, relationship of anus and external ureteric pore not determined. Heart (H) short, parallel to hindgut, less than  $\frac{1}{3}$  length of rectal kidney lobe. Principal pulmonary vein (PV) very narrow and unbranched.

Apical genitalia not observed. Hermaphroditic duct (fig. 93h, GD) a narrow, iridescent tube, partly convoluted, narrowing abruptly before reflexing to enter slightly below head of talon (GT).



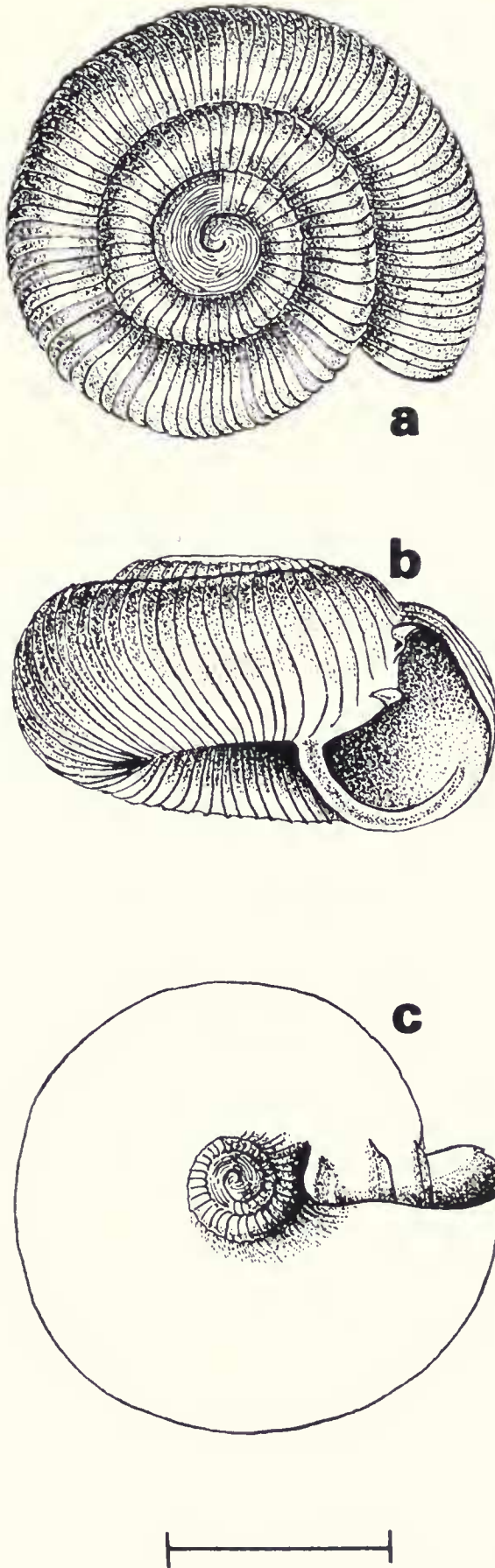


FIG. 96 a–c, *Palline biakensis*, new species. Biak Island, West Irian. Holotype. Rijksmuseum van Natuurlijke Historie, Leiden. Scale line equals 1 mm. (SG).

Albumen gland (GG) short and compact. Prostate (DG) and uterus (UT) without unusual features insofar as observation was possible.

Vas deferens (VD) very slender for entire length, reflexing upward at penioviducal angle, passing through penial retractor muscle (PR) before entering laterally on penis head. Penial retractor arising on diaphragm, very short, inserting directly on penis head after enfolding vas deferens. Penis (P) grossly expanded, enlarged portion about 0.67 mm. long, followed by a shorter, very slender tubular portion leading to atrium (Y). Expanded portion of penis basically as in *Palline notera*, covered by a thin muscle sheath, a muscular verge occupying head portion, circular pilasters in lower chamber, but with a distinct lateral shift of thin-walled portion with the 2 concentric rings of stimulatory pilasters. Atrium very slender, rather short.

Free oviduct (UV) scarcely wider than upper portion of spermathecal shaft, vagina (V) and base of spermathecal shaft grossly expanded and thick-walled with many longitudinal pilasters. Head of spermatheca (S) elongate-ovate, upper shaft very slender, twisted under uterus and prostate as shown in Figure 93b.

Buccal mass elongated with prominent generative sac. Buccal retractor inserting in U-shaped fan about  $\frac{1}{4}$  of way from posterior end. Esophagus originating slightly behind midpoint of buccal mass, a rather large diameter tube extending along inner margin of whorl to above pallial cavity apex. Stomach extending slightly more than  $\frac{1}{2}$  whorl, occupying parietal and  $\frac{2}{3}$  of palatal walls. At apex stomach narrows slightly before reflexing downward to intestine, junction narrowed by entrance of digestive gland collecting tubules. Intestine following baso-columellar margin forward to base of kidney, looping upward across kidney to midpoint of whorl, curving backward to near stomach, then looping up to parietal-palatal margin and turning forward as hindgut to pneumostome.

Free muscle system normal and compact. Right ommatophoral retractor passing through penioviducal angle, joining rhinophoral retractor halfway to union with tail fan. Buccal retractor not split, joining columellar retractor near apex.

(Based on BPBM 157731, 1 broken individual.)

#### Subfamily SEMPERDONINAE, new subfamily

A diagnosis of this subfamily has been given on p. 70.

Three genera from the Palau and Mariana Islands show a different pattern of anatomical structure in the male terminalia. Although the apical and midvisceral genitalia show no unusual features, the vas deferens starts as a very large and thin-walled tube that gradually tapers to the penioviducal angle before becoming the slender, muscular opaque tube typical of this organ. The ascending arm of the vas is not bound to the penis and enters at or near the head of the epiphallus through a simple pore. The epiphallus is a generally long, often coiled, double tube, the outer a thin muscle sheath and the inner a thick glandular tube usually rolled inward on one side. This continues into a unique muscular collar coming up from the penis sheath, with the epiphallus narrowing upon entering the collar and opening into the penis through a simple pore. The penial retractor muscle arises from the diaphragm and inserts directly onto the epiphallic head. Although varying in shape and length, the penis consists of an outer, usually very heavy sheath of circular muscles and an attached inner tube with fine apical pilasters (except *Himeroconcha rotula*) that coalesce into three variously shaped high glandular pilasters lower down (except *Ladronellum mariannarum*). The penis sheath in subadults surrounds the penis area below the

epiphallic pore, but apparently (p. 243) sexual maturity is indicated by a thickening of the penis sheath and upward extension around the base of the epiphallus, producing the "collared" effect seen in the genital illustrations (figs. 100k, 102a, 103c-d).

Variation in the functioning surfaces of the penis almost certainly relates to species isolating mechanisms. All genera agree in having very thin platelike lamellae radiating longitudinally from the epiphallic pore. In two genera, *Himeroconcha* and *Semperdon*, these coalesce, after varying space intervals, into three much larger, glandular, pilasters. In most species these three are long and finger-like, differing slightly in width and length, but in *Semperdon rotanus* (fig. 100f) they are very short, much broader than long, and teardrop-shaped. *Ladronellum mariannarum* differs only in having the initial thin pilasters unite into a single horseshoe-shaped pilaster (fig. 102d) that can be greatly swollen by fluids and when collapsed has multifolded walls. This is a modification of the basic pattern and not a major alteration.

Pallial regions in *Himeroconcha* and *Ladronellum* agree in having the kidney lobes equal or with less than a 20% differential in length, but with the pericardial lobe distinctly narrowed (fig. 102c). *Semperdon* has the kidney lobes of equal width, but the rectal lobe (fig. 100a) is more than twice the length of the pericardial. In all three genera the thickest part of the kidney laps across the hindgut and onto the parietal wall. In all fully dissected forms the pallial cavity extends about three-quarters of a whorl apically. Almost certainly this is reduced in *Himeroconcha lamlanensis*, which has only  $3\frac{1}{2}$  whorls, and probably the cavity is lengthened in *Semperdon kororensis*, which averages  $5\frac{1}{2}$  whorls. Only fragmentary, extracted specimens of these two species were available for study, so the actual pallial cavity length is unknown.

I have no doubt that these genera are a monophyletic assemblage whose penial differences result from local selective interactions. Conchologically, the genera are quite distinctive (table LIII). *Semperdon* contains the three smallest species, plus one large species. The shells (figs. 97-99, 101, 104-105) have typical radial ribbing (except *S. kororensis* with a reduced number of very large ribs), at most reduced secondary spiral cording, usually a large number of very prominent apertural barriers (except *S. uncatus*), and a flammulated color pattern (secondarily red in *S. heptptychius*). *Ladronellum* contains one species with a very high spire, few and widely spaced radial ribs, no secondary spiral cording, three small apertural barriers, and a very dark coloration. *Himeroconcha* contains four species, one with reduced sculpture and a depressed spire and three with elevated spires and very prominent secondary spiral cording. All lack apertural barriers, tend toward reduction or loss of major ribbing, are very large, tend toward development of peripheral keels, and have a dark monochrome coloration.

*Semperdon* is found on several of the Palau Islands and has been collected on Guam and Rota in the Marianas. Possibly it may be found on either Tinian or Saipan. I am not certain whether there has been sufficient collecting on these islands to have discovered *Semperdon*. Possibly Tinian and Saipan may lie outside its range. *Himeroconcha* and *Ladronellum* are restricted to Guam. All three genera have been collected together on the summit of Mt. Lamalan at about 1,300 ft. elevation. At his Station 137 in late November 1949, Yoshio Kondo collected 112 *Ladronellum mariannarum*, 23 *Himeroconcha fusca*, one *H. lamlanensis*, and three *Semperdon heptptychius*. Differences in the functional genitalia of these species are discussed elsewhere (p. 257).

### Genus *Semperdon*, new genus

Shell average to large in size, with means of  $4\frac{1}{8}$  to  $5\frac{1}{8}$  normally to tightly coiled whorls. Apex and spire slightly to strongly elevated, body whorl descending much more rapidly, spire protrusion about  $\frac{1}{7}$ - $\frac{1}{4}$  body whorl width. Apical sculpture of fine spiral cords, averaging 10-13. Postnuclear whorls with very widely spaced and few (*kororensis*) to rather numerous and crowded (*xyleborus*, some *heptptychius*) vertically to protractively sinuated radial ribs. Microsculpture of numerous fine radial and finer spiral riblets, secondary spiral cording absent except for early postnuclear whorls in *heptptychius* and *xyleborus*. Umbilicus broadly U-shaped, last whorl decoiling more rapidly, closed in *kororensis*. Sutures deep, whorls strongly rounded above, compressed laterally. Parietal barriers 2-4, generally large and prominent (reduced in *uncatus*) with or without accessory traces. Columellar wall with 0-2 barriers. Palatal barriers usually 4-8, high and near lip edge, only 0-1 in *uncatus*. Pallial cavity extending about  $\frac{2}{3}$  whorl apically, rectal kidney arm twice length of pericardial and extending across hindgut onto parietal wall. Ovary with 1 or 2 clumps of acini. Midvisceral genitalia rather short, prostatic acini few and very large. Vas deferens wide at first and thin-walled to penioviducal angle, becoming very slender and with opaque muscular walls during ascent along penis before entering head of epiphallus alongside penial retractor muscle insertion. Epiphallus a long, thick, coiled double tube entering penis through a simple pore. Penis with thick muscular sheath extending up to form a collar around base of epiphallus and extending down to end or near to end of expanded penis head, lower portion a relatively slender tube. Interior of penis with numerous very high and narrow pilasters radiating from epiphallic pore to coalesce medially in expanded section to 3 generally long and slender glandular pilasters (short and wide in *rotanus*). Free oviduct very short, spermatheca typical, vagina long and tapering.

*Type species.*—*Semperdon xyleborus*, new species.

Both *Himeroconcha* (figs. 104-105) and *Ladronellum* (fig. 101) differ conchologically in their reduced ribbing, darker monochromatic coloration on the lower spire and body whorl, rounded to keeled but not laterally compressed periphery, and absence of apertural barriers (*Himeroconcha*) or in having only a few low and broadly rounded barriers (*Ladronellum*). *Semperdon* has prominent radial ribbing, usually a flammulated color pattern, laterally compressed periphery, and very high and slender, usually numerous, apertural barriers. The Trukcharopinae differ in having prominent secondary spiral cording in the microsculpture and monochromatic coloration; they usually lack apertural barriers or have them peculiarly twisted



TABLE LIII. - RANGE OF VARIATION IN SEMPERDONINAE.

NAME	NUMBER OF SPECIMENS EXAMINED	RIBS	RIBS/MM.	HEIGHT	DIAMETER	
<u>Semperdon</u>						
<u>kororensis</u> (Beddome)	13	24.5(18-32)	1.70(1.29-2.29)	3.12(2.73-3.59)	4.59(4.05-5.16)	
<u>xyleborus</u>	173	104.0(88-120)	12.04(9.68-15.65)	1.56(1.38-1.74)	2.88(2.67-3.19)	
<u>uncatus</u>	16	78.0(56-102)	9.81(6.99-13.54)	1.68(.158-1.74)	2.83(2.53-3.03)	
<u>rotanus</u>	205	76.0(60-95)	8.22(6.68-9.98)	1.53(1.26-1.76)	2.95(2.48-3.21)	
<u>heptaptychius</u> (Q. & M.)	1,310	75.3(35-131)	7.84(2.97-13.59)	1.68(1.58-1.74)	3.32(2.47-5.17)	
<u>Ladronellum</u>						
<u>marianarum</u> (Q. & M.)	152	51.8(46-62)	4.80(4.16-5.61)	2.39(1.84-2.93)	3.66(3.03-4.28)	
<u>Himeroconcha</u>						
<u>lamlamensis</u>	2	31-35 IRREGULAR	-----	1.85(1.79-1.92)	3.96(3.94-3.97)	
<u>rotula</u> (Q. & M.)	25	34-42 REDUCED	-----	2.27(2.01-2.70)	4.57(4.05-5.53)	
<u>quadrasi</u> (Mlildf.)	15	REDUCED	-----	2.23(2.03-2.45)	4.85(4.54-5.13)	
<u>fusca</u> (Q. & M.)	40	REDUCED	-----	2.84(2.17-3.36)	6.13(5.59-7.04)	
	H/D RATIO	WHORLS	UMBILICUS	D/U RATIO	APICALS	SPIRE ELEVATION
<u>koror.</u>	0.678(0.615-0.717)	5 1/8(4 1/2-5 1/2)	LATERAL CRACK	-----	13.2(11-14)	0.46
<u>xyleb.</u>	0.546(0.512-0.574)	4 1/2+(4 1/4-4 3/4)	0.84(0.76-0.95)	0.35(3.17-3.57)	13.0(12-14)	0.13(0.07-0.23)
<u>uncat.</u>	0.599(0.539-0.675)	4 5/8+(4 1/2-4 7/8)	0.72(0.53-0.82)	3.98(3.68-4.81)	10.0(9-11)	0.23(0.13-0.33)
<u>rotan.</u>	0.518(0.452-0.570)	4 1/8+(4-4 5/8)	0.73(0.53-0.92)	3.92(3.22-5.25)	9.9(8-12)	0.16(0.10-0.20)
<u>hepta.</u>	0.490(0.394-0.570)	4 1/2-(4-5 1/8)	0.99(0.53-1.91)	3.44(2.69-4.94)	10.5(8-13)	0.17(0.07-0.33)
<u>maria.</u>	0.652(0.590-0.780)	4 5/8-(4 1/4-5 1/8)	0.97(0.69-1.25)	3.77(3.24-4.76)	10.5(9-13)	0.41(0.26-0.63)
<u>lamla.</u>	0.469(0.450-0.487)	3 1/2+(3 1/2-3 5/8)	1.51(1.12-1.18)	3.43(3.31-3.54)	7.5(7-8)	DEPRESSED
<u>rotula</u>	0.497(0.440-0.554)	4 1/4+(4-4 5/8)	1.30(1.05-1.58)	3.51(3.17-4.06)	8.7(7-11)	0.23(0.20-0.28)
<u>quadr.</u>	0.461(0.419-0.496)	4 3/8-(4 1/8-4 5/8)	1.33(1.05-1.58)	3.70(3.12-4.56)	9.7(8-12)	0.22(0.13-0.30)
<u>fusca</u>	0.464(0.388-0.550)	4 1/2+(4 1/4-4 3/4)	1.39(1.05-1.63)	4.44(4.00-5.81)	10.2(8-12)	0.35(0.33-0.40)
		BODY WHORL WIDTH	SP/BWW	PR	C	P
<u>koror.</u>	1.84		0.250	4+1	2	7+3-4
<u>xyleb.</u>	0.92(0.74-1.12)		0.138(0.082-0.226)	4+ <u>2</u> -3	2+ <u>0</u> - <u>1</u> -2	7- <u>8</u> +3- <u>4</u> - <u>5</u>
<u>uncat.</u>	1.00(0.92-1.09)		0.230(0.143-0.345)	2	<u>0</u> - <u>1</u>	<u>0</u> -1
<u>rotan.</u>	0.99(0.92-1.05)		0.158(0.097-0.200)	3+1	1-2	<u>4</u> - <u>5</u> - <u>6</u> -7- <u>8</u> - <u>9</u> - <u>10</u>
<u>hepta.</u>	1.01(0.92-1.32)		0.170(0.068-0.345)	<u>2</u> -3+ <u>0</u> -1	<u>0</u> -1-2- <u>3</u>	<u>3</u> - <u>4</u> - <u>5</u> - <u>6</u> - <u>7</u> - <u>8</u>
<u>maria.</u>	1.26(1.05-1.38)		0.329(0.242-0.442)	1	<u>0</u> -1	<u>0</u> -1
<u>lamla.</u>	1.15		-----	0	0	0
<u>rotula</u>	1.30(1.25-1.38)		0.181(0.154-0.208)	0	0	0
<u>quadr.</u>	1.27(1.12-1.40)		0.173(0.108-0.243)	0	0	0
<u>fusca</u>	1.49(1.35-1.66)		0.234(0.213-0.256)	0	0	0

(*Jokajdon*), much shorter (*Palline*), or reduced in number (*Palikirus*, *Roimontis*).

Anatomical differences are more significant. Genera of the Trukcharopinae lack any epiphallus and, except for *Jokajdon*, have the vas deferens passing through the penial retractor muscle before entering

the penis head. *Himeroconcha* and *Ladronellum* differ from *Semperdon* in having the rectal kidney lobe at most 20% longer than the pericardial, which is noticeably narrowed. In *Himeroconcha lamlanensis*, where the whorl count is greatly reduced to 3½, the kidney lobes are equal in length. *Semperdon* (fig. 100a) has

the rectal kidney lobe more than twice the length of the pericardial, which is not narrowed. In *Himeroconcha* and *Ladronellum* the vas deferens enters the epiphallus slightly below the rounded head (fig. 102d) and distinctly away from the point of penial retractor insertion; in *Semperdon* the vas deferens enters the epiphallus head itself right next to one end of the penial retractor insertion (fig. 100i).

Five species are recognized, *S. rotanus* and *S. heptptychius* from Rota and Guam in the Marianas; *S. uncatus*, *S. xyleborus*, and *S. kororensis* (Beddome) from the Palau Islands. In the latter group, all three species have been found on Koror, but only two, *S. kororensis* and *S. xyleborus*, at the same station. Both *S. uncatus* and *S. xyleborus* have been collected on Angaur at Station 175. The two Marianas species have not been shown to be sympatric.

Although there are no obvious major anatomical differences between the Palau and Marianas species, there are conchological changes, primarily in the whorl contours and apertural barriers. The Palau species have the sculpture vertically sinuated; the Marianas species have the sculpture protractively sinuated. The Palau species have the upper parietal bifid or twisted downward on the posterior portion, and all barriers are slender, at most weakly expanded above; the Marianas species have the upper parietal neither bifid nor twisted downward, and all barriers tend to be bulbously expanded above. The Palau species tend to have slight lateral flattening of the body whorl, if any departure from the evenly rounded periphery occurs; the Marianas species tend to lateral flattening above the periphery and on the basal margin if departures occur from the rounded periphery. Because only *S. xyleborus* of the Palau species has had the apical genitalia examined, I am not sure what importance to assign the presence of two ovotestis clumps in that species compared with the one clump in both Marianas *Semperdon*. Possibly more complete anatomical study may show that a phylogenetic gap exists between the Palau and Marianas species, but I see no evidence suggesting systematic separation at this time.

Differences among the Palau species are relatively obvious. *Semperdon uncatus* is apt to be confused with *Palline notera* (p. 228) and has much fewer apertural barriers than the other species. *Semperdon xyleborus* and *S. kororensis* (fig. 98a–f) have nearly identical apertural barriers, but differ obviously in the altered size, closed umbilicus, and very few and widely spaced radial ribs of the latter species. *Semperdon rotanus* (fig. 99d) has rounded whorls with only a slight trace of lateral flattening above the periphery and averages seven palatals; *S. heptptychius* (fig. 99a–c) has marked lateral flattening of the body whorl both above the periphery and on the basal margin and averages only four palatals. Individuals of both species (table LV, p. 241) have palatal barrier counts in the range of the other, but differences in the whorl contours, size, and umbilical width enable identification of doubtful

specimens. Specific separation is on the basis of a marked difference in penial structure (p. 247). Although the two species are not known to be sympatric, the altered penial structure in *S. rotanus* strongly suggests that sympatry existed at least in the past. Collections in the vicinity of Ritidian Point in northern Guam might enable study of the two species under sympatric conditions.

***Semperdon uncatus*, new species. Figures 97a–c, 100k.**

*Diagnosis.*—Shell of average size, diameter 2.53–3.03 mm. (mean 2.83 mm.), with  $4\frac{1}{2}$ –4% tightly coiled whorls. Apex and spire moderately to strongly and evenly elevated, body whorl descending somewhat more rapidly, spire protrusion a little less than  $\frac{1}{4}$  body whorl width, H/D ratio 0.539–0.675 (mean 0.599). Apical sculpture of 9–11 (mean 10.0) prominent spiral cords, whose interstices are 3–4 times their width. Postnuclear whorls with high, narrow, prominent, almost vertically sinuated radial ribs, 56–102 (mean 78.0) on the body whorl, whose interstices are 3–6 times their width. Ribs/mm. 6.99–13.54 (mean 9.81). Microsculpture of extremely fine microradial and spiral riblets, usually more than 7 between each pair of major ribs, but accurate counts at 96 $\times$  magnification were not possible. No secondary spiral cording evident. Umbilicus rather widely open, U-shaped, last whorl decoiling more rapidly, contained 3.68–4.81 times (mean 3.98) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above and on basal margin, slightly compressed laterally with evenly rounded outer margin. Aperture ovate, inclined about 5° from shell axis. Parietal barriers 2, low, short, extending posteriorly about  $\frac{1}{6}$  whorl; upper a thin blade, more elevated, slightly expanded and twisted downward on posterior third, with gradual descension to threadlike anterior quarter; 2nd a very low and broadly rounded threadlike ridge extending slightly further anteriorly. Columellar wall usually (83%) barrier-free, often (17%) with a low, threadlike ridge reaching top of weak columellar callus. Palatal wall normally (83%) with, often (17%) without, a short, low, crescentic, broadly rounded barrier on basal lip, extending about  $\frac{1}{6}$  whorl, reaching lip margin. Columellar callus extending only slightly onto basal lip.

*Semperdon uncatus* (fig. 97a–c) differs from all races of *Palline notera* (figs. 94a–f, 95a–b) in its much larger size, reduced apertural callus, absence of secondary spiral cording, and in having only one barrier on the outer wall of the aperture. All other *Semperdon* have at least three large palatals (usually more) and much larger parietals.

*Description.*—Shell of average size, with  $4\frac{3}{4}$  moderately tightly coiled whorls. Apex and spire moderately elevated, flatly rounded above, H/D ratio 0.577. Apical whorls  $1\frac{1}{2}$ , sculpture of 9 prominent, rather widely spaced spiral cords. Postnuclear whorls with vertically sinuated, prominent, narrow, rather crowded radial ribs, 102 on the body whorl, whose interstices are 2–4 times their width. Microsculpture mostly eroded, but traces of fine microradial and spiral ribbing visible. Sutures relatively deep, whorls evenly rounded on outer margin, compressed laterally. Umbilicus U-shaped, decoiling regularly at first, last whorl more rapidly, contained 3.68 times in the diameter. Color leached from shell except for vague traces of reddish maculations. Aperture ovate, almost parallel to shell axis. Parietal barriers 2, extending posteriorly about  $\frac{1}{6}$  whorl, low and threadlike: upper elevated and weakly expanded, slightly twisted downward on posterior 3rd, middle 3rd gradually descending. Basal lip with single knoblike barrier, slightly recessed from apertural margin. Height of holotype 1.74 mm., diameter 3.03 mm.

*Holotype.*—Palau Islands: Angaur, Station 175, edge of guano pit, north of shrine at 75–100 ft. eleva-



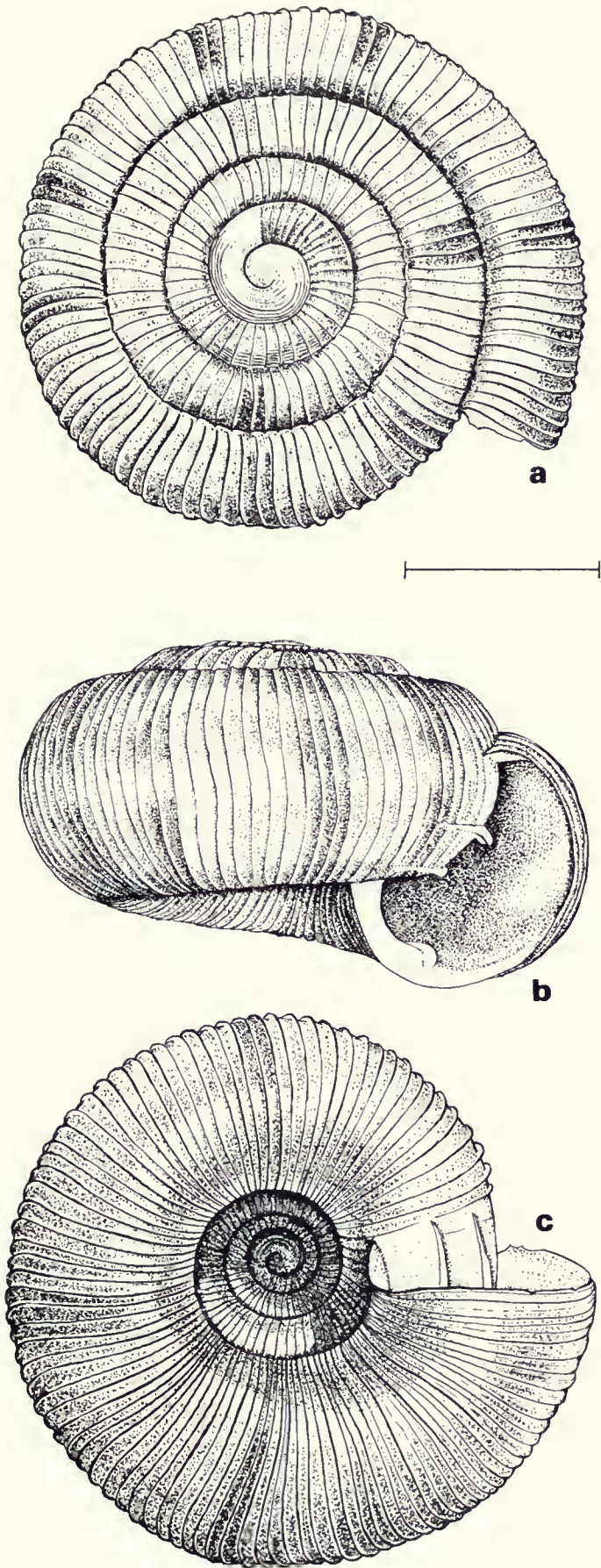


FIG. 97. a–c, *Semperdon uncatus*, new species. Station 175, Angaur, Palau Islands. Holotype. BPBM 158309. Scale line equals 1 mm. (SH).

tion. Collected by Kiyoko and Yoshio Kondo on April 18, 1936. BPBM 158309.

*Range*.—Angaur, Koror, and Auluptagel, Palau Islands.

*Paratypes*.—Angaur: edge of guano pit north of shrine (Station 175) at 75–100 ft. elevation (12 specimens, BPBM 158263, BPBM 158309). Koror: hillside above Komakan (Station 222) at 100–200 ft. elevation (1 specimen, BPBM 154850). Auluptagel: Aurapushekuru (Station 230) at 5–90 ft. elevation (1 specimen, BPBM 159148); northwest end of island, 100 yd. inland at 140 ft. elevation (1 specimen, USNM, collected by H. S. Ladd on March 16, 1958).

*Remarks*.—The two specimens from Auluptagel are much higher and more narrowly umbilicated than the shells from Angaur (table LIV). One of the Auluptagel shells (USNM) has a distinct columellar but no palatal barriers. Neither specimen was in good condition, so I have chosen to lump these populations although realizing they may be subspecifically distinct.

*Palline notera* (figs. 94a–f, 95a–b) and *Semperdon uncatus* (fig. 97a–c) can easily be confused. The small apertural barriers of the *Semperdon* can be interpreted as being derived from the *Palline* complex by simple size reduction and loss of some barriers. On initial conchological inspection, I had considered them to be closely related. Dissection of a single specimen of *S. uncatus* showed that it has the terminal genital structure found in the *Semperdoninae* rather than the *Trukcharopinae*. Classification in *Semperdon* is the most reasonable alternative, despite the vastly greater number of apertural barriers in the other species.

Shell differences of *S. uncatus* from *Palline notera* are relatively inconspicuous, involving reduction of the columellar-palatal callus to a trace, absence of secondary spiral cording, presence of only 10 apical cords (instead of 12.4–13.3), reduction in barrier height and length, slightly larger size, reduced lateral compression of the body whorl, and noticeably increased whorl count. Because some endodontine species have exceptionally large gerontic examples with reduced apertural barriers, for example, *Minidonta simulata* Solem & Cooke (Solem, 1976b, p. 147, fig. 70d), specimens of *Semperdon uncatus* could be taken as gerontic individuals of *Palline notera* unless extreme care is taken to notice whether there is prominent secondary spiral cording.

Both *Semperdon xyleborus* and *S. uncatus* have been taken at Station 175 on Angaur. The expanded penis muscle sheath area appears proportionately shorter and the epiphallus much longer and narrower in *S. uncatus*. Without more material of the latter, it will be impossible to determine if these are the isolating characters between the two species. *Semperdon kororensis* and *S. uncatus* were collected at Station 222 on Koror, but the adult genital anatomy of the former species is unknown. The size difference between the two species is so large that simple size alterations may result in maintenance of species isolation.

## SOLEM: ENDODONTOID LAND SNAILS

TABLE LIV. - LOCAL VARIATION IN PALAU ISLAND SEMPERDON.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER	H/D RATIO
<u>xyleborus</u>						
Peleliu Sta. 184 BPBM 159516	4	107.3±6.41 (97-126)	11.20±0.869 (9.68-13.70)	1.68±0.028 (1.62-1.76)	3.08±0.056 (2.95-3.21)	0.547±0.0060 (0.532-0.562)
Koror Sta. 213 BPBM 158964	1	-----	-----	1.38	2.66	0.518
Sta. 212 BPBM 159108	1	94	12.81	1.18	2.34	0.507
Angaur Sta. 175 BPBM 158261-2	4	105	12.40	1.52±0.045 (1.39-1.59)	2.75±0.033 (2.72-2.85)	0.555±0.015 (0.512-0.574)
Ngemelis Sta. 210, Juv. BPBM 159231	3	115	15.67	1.23±0.033 (1.19-1.29)	2.20±0.080 (2.09-2.35)	0.558±0.0069 (0.549-0.572)
<u>kororensis</u>						
Sta. 222 BPBM 154842,6-7	6	25.5±1.86 (20-32)	1.81±0.169 (1.50-2.23)	3.17±0.107 (2.91-3.61)	4.56±0.139 (4.07-5.03)	0.696±0.0082 (0.669-0.717)
BPBM 91.3.17.12	1	25	1.54	3.29	5.16	0.637
BPBM 167441	1	18	1.29	2.73	4.44	0.615
<u>uncatus</u>						
Angaur Sta. 175 BPBM 158309	3	102	10.71	1.69±0.051 (1.59-1.76)	3.01±0.033 (2.95-3.05)	0.560±0.0110 (0.539-0.577)
Auluptagel Sta. 230 BPBM 159148	2	61.0 (56-66)	7.52 (7.05-7.99)	1.71 (1.68-1.74)	2.58 (2.53-2.63)	0.656 (0.637-0.675)
		WHORLS	UMBILICUS	D/U RATIO	APICAL RIBS	
<u>xyleborus</u>						
Peleliu Sta. 184	4	5/8+(4 5/8-4 3/4)	0.93±0.025 (0.86-0.95)	3.29±0.055 (3.17-3.42)	13.67±0.334 (13-14)	
Koror Sta. 213	4	3/8-	0.79	3.38	-----	
Sta. 212	4	1/2	0.72	3.23	12	
Angaur Sta. 175	4	1/2+(4 1/2-4 3/4)	0.80±0.021 (0.76-0.86)	3.43±0.055 (3.31-3.57)	-----	
Ngemelis Sta. 210	4+	(4-4 1/8)	0.58±0.029 (0.53-0.63)	3.76±0.098 (3.61-3.94)	12	
<u>kororensis</u>						
Sta. 222	5	1/4+(5-5 1/2)	IMPERFORATE	-----	13.0±0.546 (11-14)	
BMNH	5	1/4	IMPERFORATE	-----	10	
BPBM	4	1/2	IMPERFORATE	-----	14	
<u>uncatus</u>						
Angaur Sta. 175	4	3/4-(4 3/8-4 7/8)	0.81±0.011 (0.79-0.82)	3.69±0.0098 (3.68-3.71)	-----	
Aulupt. Sta. 230	4	5/8(4 1/2-4 5/8)	0.60 (0.53-0.66)	4.40 (4.00-4.81)	9	

The name *uncatus*, meaning bent inward or hooked, refers to the twisted portion of the upper parietal barrier.

*Description of soft parts.*—One fragmentary, squashed individual examined. Foot and pedal grooves typical, no caudal horn or caudal foss developed.

Body color light yellow-white, without darker markings.

Mantle collar narrow, rounded anteriorly, no protrusion of man-

tle glands onto pallial roof. Anterior tip of rectal kidney arm and secondary ureter seen, but apical portion of pallial cavity not available. Sufficient pallial roof tissue present to determine that rectal kidney arm was longer than pericardial.

Apical genitalia not seen. Lower part of prostate with very large acini, expanded and thick-walled lower uterine chamber typical. Vas deferens (VD) enlarged at base of prostate, broken off in specimen with most of length missing, remnant of a very thin tube entering head of epiphallus just to side of penial retractor muscle (fig. 100k,



TABLE LV. - SUMMARY OF BARRIER VARIATION  
IN MARIANAS ISLANDS SEMPERDON.

	<u>heptptychius</u>	<u>rotanus</u>
Parietals		
2	5.1%	100%
3	3.3%	
3+1	91.3%	100%
3+2	0.3%	
Columellars		
0	0.3%	
1	42.1%	46.5%
2	56.4%	53.5%
3	1.2%	
Palatals		
3	1.2%	
4	80.0%	1.4%
5	13.1%	2.8%
6	3.9%	19.8%
7	1.5%	55.0%
8	0.3%	14.0%
9		5.6%
10		1.4%
Total specimens tallied	335 adults	71 adults

PR), which is very short and arises from diaphragm. Epiphallus (E) a long, cylindrical tube appearing to have high longitudinal pilasters (presumably with invaginated tube), entering globular penis sheath (PS). Penis area artificially flattened in preservative before dissection, very short, about 0.5 mm. long, internally with tube of epiphallus expanding and pilasters splitting into many narrow ones that taper toward end of muscle sheath. Length of post-muscle sheath penial tube unknown.

Free oviduct somewhat bulbous just below uterus, internally with longitudinal pilasters, tapering to junction with spermatheca. Duct of spermatheca lying along acini of prostate, head missing, shaft expanding rapidly from point just above head of vas deferens, grossly enlarged to union with free oviduct, walls thick and glandular. Vagina a rather long, thin-walled tube, equal in diameter to free oviduct, walls thick and glandular. Vagina a rather long, thin-walled tube, equal in diameter to free oviduct.

(Based on BPBM 154850, 1 fragmentary individual.)

**Semperdon xyleborus**, new species. Figures 98d–f, 100g–j.

**Diagnosis.**—Shell of average size, diameter 2.67–3.19 mm. (mean 2.88 mm.), with  $\frac{3}{4}$ – $\frac{4}{5}$  tightly coiled whorls. Apex and early spire slightly elevated, lower whorls descending more rapidly, body whorl even more rapidly, spire protrusion about  $\frac{1}{2}$  body whorl width, H/D ratio 0.512–0.574 (mean 0.546). Apical sculpture of 12–14 (mean 13.0) fine spiral cords, whose interstices are 2–4 times their width. Postnuclear sculpture of high, prominent, crowded, lamellar, protractively sinuated radial ribs, 88–120 (mean 104.0) on the body whorl, whose interstices are 2–4 times their width. Microsculpture of fine radial riblets, 5–10 between each pair of major ribs, crossed by distinctly finer and more crowded spiral riblets, traces of crowded

secondary spiral cording visible on spire and shell base although not visible on body whorl. Umbilicus broadly U-shaped, last whorl de-coiling somewhat more rapidly, contained 3.17–3.57 times (mean 3.35) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above and on basal margin, very slightly compressed laterally above and below evenly rounded periphery. Aperture ovate, slightly compressed laterally above and below periphery, inclined less than  $10^\circ$  from shell axis. Parietal barriers 4, extending posteriorly more than  $\frac{1}{2}$  whorl, usually with 3 (84.6%), often with 2 (15.4%) accessory traces: upper parietal a high, thin blade, flat above on posterior  $\frac{2}{3}$  with rather sharp anterior descension, posterior portion varying from rolled and expanded, partly twisted downward, to with a distinct accessory lamella on lower side of barrier, under last 2 conditions with upper half of main blade distinctly curved upward; 2nd equal in height and slightly expanded above on posterior quarter to half, with more gradual anterior descension to point slightly beyond upper parietal; 3rd higher than 2nd, flat on posterior half with broad expansion above, gradually descending until just before anterior termination beyond end of 2nd; 4th greatly reduced in height, moderately to strongly expanded above on posterior 3rd to half with gradual descension over anterior quarter. Accessory traces very narrow, raised, bladelike lamellae, usually 2 situated between upper parietal and parietal-palatal margin that are not expanded posteriorly, 3rd below 4th parietal just above columellar margin and moderately expanded on posterior half. Columellar wall with 2 long barriers and usually 2 accessory traces, occasionally 1 or both of the latter absent: upper columellar a thin, moderately elevated blade, lying parallel to plane of coiling, sometimes moderately expanded above on posterior half, with abrupt, rather sinuately twisted anterior descension across columellar callus to lip edge; 2nd up to twice as high, crescentic, slanting  $45^\circ$  downward from plane of coiling, broadly expanded and serrated on middle half to two-thirds, with very abrupt anterior descension to lip edge and slight inward turn of tip. Accessory traces located above upper columellar, very thin and low V-shaped traces that are variously angled across columellar callus almost to lip edge. Palatal barriers short, normally (92%) 7, occasionally (8%) 8, progressively further recessed from lip edge, with 3 (85%), 4 (7.5%) or 5 (7.5%) accessory traces above upper palatal: lower palatal very high, crescentic, basal in position, pointing toward outer edge of 3rd parietal, shape, expansion, and anterior descension agreeing with 2nd columellar; 2nd through 6th progressively more deeply recessed, with flattening increasingly restricted to posterior portions, more gradual anterior descension, and lessened expansion above; normally 2nd through 6th palatals show gradual decrease in height, but in those where the upward twist of the 1st parietal is accentuated, the 5th and 6th palatals increase in height; 7th palatal much lower, shorter, more deeply recessed, expanded and elevated portion restricted to posterior quarter, with very gradual anterior descension. Palatal traces short, deeply recessed, very thin, low, lying between 7th palatal and palatal-parietal margin.

*Semperdon xyleborus* (fig. 98d–f) is most similar to *S. kororensis* (fig. 98a–c). The latter is much larger (table LIII), has a closed umbilicus, few and very widely spaced radial ribs, and is a much more elevated shell. *Semperdon rotanus* (fig. 99d) has fewer and more widely spaced radial ribs, a narrower umbilicus, and fewer apical cords. *Semperdon heptptychius* (fig. 99a–c) has much fewer and more expanded palatal barriers, is strongly flattened laterally above the periphery, and has only two or three major parietals.

**Description.**—Shell of average size, with  $\frac{4}{5}$  moderately tightly coiled whorls. Apex flat, whorls of spire descending moderately, last whorl much more rapidly, H/D ratio 0.546. Apical whorls  $1\frac{1}{2}$ , sculpture of 14 fine spiral cords. Postnuclear whorls with broadly rounded, protractively sinuated radial ribs, 103 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets, 5–10 between each pair of major ribs, crossed by fine crowded spiral riblets. Secondary spiral cording present on part of shell. Sutures deeply impressed, whorls strongly rounded above, slightly flattened laterally. Umbilicus broadly opened, U-shaped,

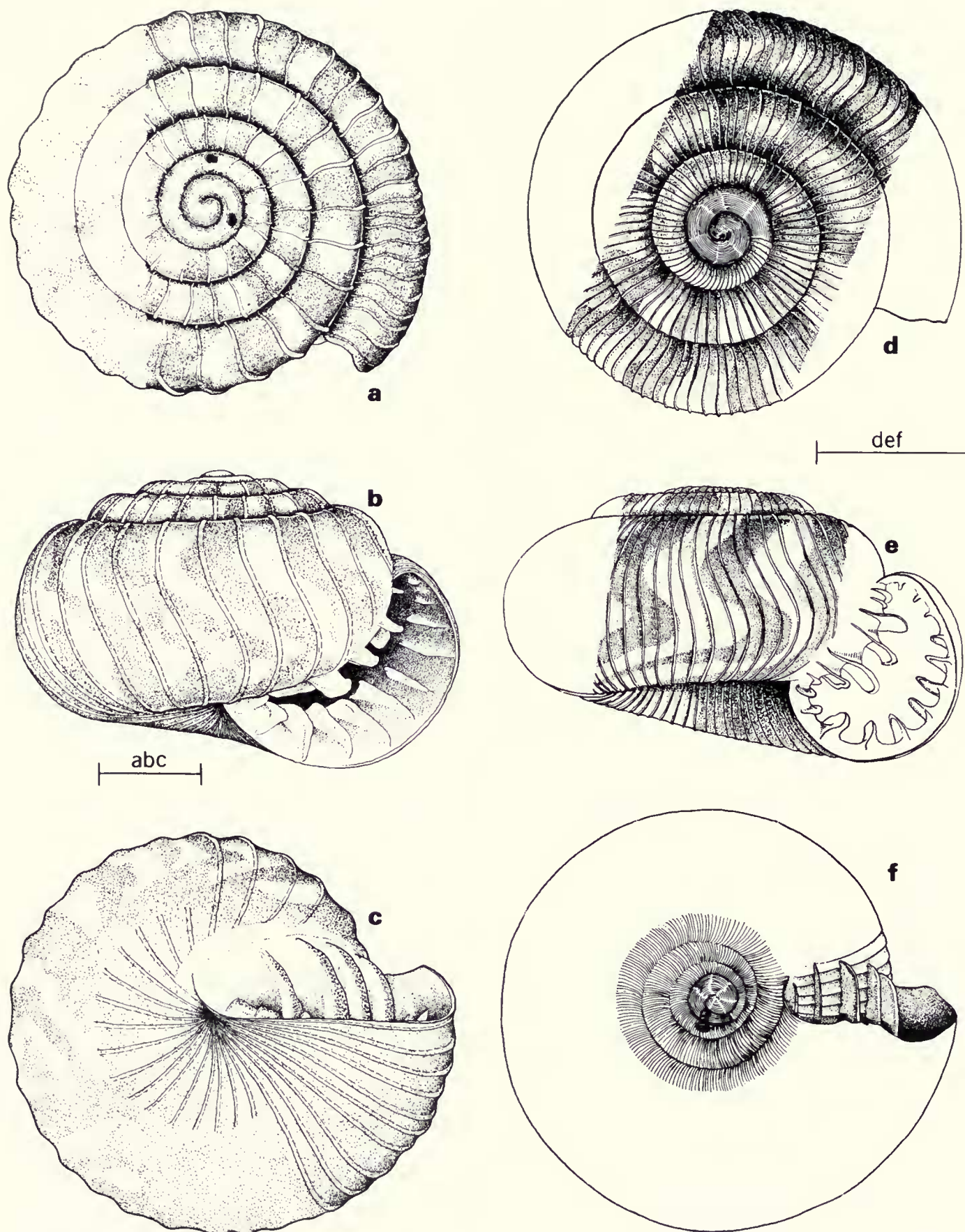


FIG. 98. **a-c**, *Semperdon kororensis* (Beddome). Station 222, Komakan, Koror, Palau Islands. BPBM 154842; **d-f**, *Semperdon xyleborus*, new species. Station 184, Peleliu, Palau Islands. Holotype. BPBM 159516. Scale lines equal 1 mm. (**a-c**, MM; **d-f**, SG).



regularly decoiling, contained 2.34 times in the diameter, margins strongly rounded. Color light yellow-brown with relatively regular, broad, reddish flammulations. Aperture elongately ovate, inclined about 5° from the shell axis. Major parietal barriers 4, extending posteriorly  $\frac{1}{8}$  whorl, with 3 accessory traces: structure as in diagnosis, with upper showing only faint posterior bifidity and moderate upward twisting. Columellar barriers 2, lower only slightly angled downward from plane of coiling, structure as in diagnosis, no accessory traces. Palatal barriers 7, short, extending less than  $\frac{1}{8}$  whorl, structure and size as in diagnosis, 3 short accessory traces above upper palatal. Height of holotype 1.68 mm., diameter 3.10 mm.

*Holotype*.—Palau Islands: Peleliu, Station 184, on damp hillside east of Station 176, 100 yd. inland at 100 ft. elevation. Collected under stones and logs by Kiyoko and Yoshio Kondo and Atietho on April 24, 1936. BPBM 159516.

*Range*.—Peleliu, Koror, Ngemelis, and Angaur, Palau Islands.

*Paratypes*.—Peleliu: east of Station 176 (Station 184), 100 yd. inland at 200 ft. elevation (33 specimens, BPBM 159516); Omurbrogol Mt. (Station 182), Asias Village,  $\frac{1}{2}$ – $\frac{3}{4}$  mile inland at 300–400 ft. elevation (5 specimens, BPBM 159429–31); near phosphate mine and 300–400 yd. north (Stations 201, 203) at 35–200 ft. elevation (8 specimens, BPBM 159950, BPBM 159995); southwest of Ngakal (Station 209) on new NKK trail up to 1,440 m., 100–150 yd. inland at 10–12 ft. elevation (1 specimen, BPBM 160091); east side, 10–80 ft. inland at 5–8 ft. elevation (2 specimens, BPBM 190405). Koror: Komakan (Stations 217, 219), south below Station 218 in pocket, 20–75 yd. inland at 5–90 ft. elevation (18 specimens, BPBM 158764, BPBM 158685); islet V (Station 213) at 10–12 ft. elevation (1 specimen, BPBM 158964); Islet XXIX (Station 212), northeast side of western neck of island, 10 yd. inland at 30–100 ft. elevation (2 specimens, BPBM 159108); in forest on limestone (1 specimen, BPBM 193145). Ngemelis: island #8 (Station 210) at 2–35 ft. elevation (13 specimens, BPBM 159230–1). Angaur: north of shrine (Station 175), edge of guano pit at 75–100 ft. elevation (90 specimens, BPBM 158261–2, BPBM 158308).

*Remarks*.—Specimens of *Semperdon xyleborus* were taken on several islands. Adults were limited in number, with five (10.2%) of 49 from Peleliu; two (9.5%) of 21 from Koror; four (4.4%) of 90 dead shells taken from a guano pit on Angaur; and none of 13 from Ngemelis showing fully adult characters. Despite the limited adult material, there is some indication of inter-island variation. The Koror shells (table LIV) are small and distinctly more depressed than those from Angaur. Peleliu examples agree with the Angaur shells in shape but are even larger. The three largest Ngemelis subadults were measured. Although the shells agree with the Angaur shells in shape, they show statistical differences in rib spacing and D/U ratio. Probably these have no systematic implications. Rib spacing tends to be more crowded on small shells, and adult characters in this species involve the more rapid decoiling of the body whorl, so that a proportion-

ately more narrow umbilicus in subadults is to be expected.

Possibly *Semperdon xyleborus* has undergone an extensive pattern of geographic subspeciation, but currently available material is totally inadequate to determine whether this has occurred.

The specific name *xyleborus* is taken from Greek "xyleboros" for "eating wood" and refers to the habitat of many endodontoids in rotting wood.

Both subadult and adult examples were dissected. In the subadults from Station 184 (BPBM 159516) the penis was swollen medially and the internal pilasters developed, but the muscle sheath was only partly developed. It enfolded the enlarged section of the penis, but did not extend upward around the epiphallallic base as a collar. Penis length, allowing for the collar absence, was identical, so it seems probable that collar development is one of the last stages in penial maturation. The comparatively large epiphallus enabled determination of internal structure. A thin outer wall of muscle surrounds a separate, thick-walled tube of glandular tissue. One edge of this tube is invaginated to past the center, producing a much greater glandular-surfaced area than with just a cylinder of equal diameter. Viewed from the exterior, this gives the appearance of two pilasters, because the opening where the edge is rolled in appears as a blank space on the outer wall.

*Description of soft parts*.—Foot and tail shorter than shell diameter. Sole and pedal grooves typical, no caudal horn or middorsal groove developed.

Body color light yellow-white, faint reddish gray markings on back of head.

Mantle collar wide, slight glandular extension onto pallial roof. Anus opening slightly in front of external ureteric pore just inside pneumostome.

Pallial region extending  $\frac{5}{8}$  whorl apically. Lung roof clear, no granulations. Kidney about 2.1 mm. long, bilobed, rectal lobe twice length of pericardial, extending across hindgut and slightly onto parietal wall. Pericardial lobe about 0.86 mm. long, equal in width to rectal. Ureter with arms tightly compacted between kidney lobes, very slender along hindgut. Heart slightly angled from hindgut, shorter than pericardial kidney lobe. Principal pulmonary vein very indistinct, unbranched. Hindgut extending apically almost  $\frac{1}{2}$  whorl above kidney apex, intestinal loop a simple, broad "S."

Ovotestis (fig. 100g, G) with 2 linear clumps of palmately clavate alveoli above stomach apex. Hermaphroditic duct (G) iridescent, simple, uncoiled, slightly expanded medially, tapering gradually to union with carrefour. Albumen gland (GG) short and compact, acini small. Talon (GT) with globular head, slender shaft longer than head, carrefour and hermaphroditic duct union as in *Ladronellum mariannarum* (fig. 102e). Prostate (DG) of a few large acini opening into groove on inner surface of prostate. Uterus (UT) bipartite, walls of lower chamber complexly folded because of epiphallallic head pressure.

Vas deferens (VD) wide and thin-walled at first, tapering to penioviducal angle, walls becoming muscular and opaque during ascent to head of epiphallus along edge of penial retractor insertion. Epiphallus (E) curved to coiled, sometimes equal in diameter to penis, relatively long, entering penis through a simple pore. Outer tube a thin muscle sheath, inner a thick-walled glandular tube with one side rolled inward. Penial retractor (PR) very short, arising from diaphragm, inserting on head of epiphallus just to side of vas deferens insertion. Penis (P) with prominent muscle sheath, about 1.2–1.4

mm. long, lower half a slender tube, upper part moderately expanded, sheath forming a collar around base of epiphallus in adults, interior of penis with typical pilasters (fig. 100j, PP). Atrium (Y) short, slightly wider than penis.

Free oviduct (UV) short and slender. Spermatheca (S) typical, slender part of shaft partly coiled around prostate-uterus, expanded head (not shown) lying next to outer palatal wall. Vagina (V) rather slender, slightly shorter than penis in length.

Free muscle and digestive systems typical.

(Based on BPBM 159516 and 158261, 3 whole shells about 2.7 mm. in diameter, and several fragmentary examples.)

**Semperdon kororensis** (Beddome, 1889). Figure 98a-c.

*Helix* (*Endodonta*) *kororensis* Beddome, 1889, Proc. Zool. Soc. London, 1889, p. 116, pl. 12, figs. 11, a-c—Koror, Palau Islands.

*Patula* (*Endodonta*) *kororensis* (Beddome), Pilsbry, 1892c, Man. Conchol., (2) 8, p. 84, pl. 30, figs. 43-45.

*Endodonta* (*Endodonta*) *kororensis* (Beddome), Pilsbry, 1893, Man. Conchol., (2) 9, p. 26.

**Diagnosis.**—Shell very large, diameter 4.05-5.16 mm. (mean 4.59 mm.) with  $4\frac{1}{2}$ - $5\frac{1}{2}$  very tightly coiled whorls. Apex and spire moderately to strongly and almost evenly elevated, usually slightly rounded above, body whorl descending much more rapidly, spire protrusion about  $\frac{1}{4}$  body whorl width, H/D ratio 0.615-0.717 (mean 0.678). Apical sculpture of 11-14 (mean 13.2) low, rounded spiral cords, whose interstices are 2-4 times their width. Postnuclear whorls with very high, narrow, sharply defined, very widely spaced, slightly protractively sinuated radial ribs, 18-32 (mean 24.5) on the body whorl, whose interstices are about 6-9 times their width, except ribs wider and more crowded near aperture. Ribs/mm. 1.38-1.74 (mean 1.56). Microsculpture of very fine radial riblets, about 25-35 between each pair of major ribs, crossed by barely visible spiral riblets, upper surface showing fine secondary spiral cords, widely spaced at first, becoming crowded and indistinct on lower whorls. Umbilicus reduced to a very narrow lateral crack, through which next 2 whorls are visible, by strong columellar reflection. Sutures very deep, whorls shouldered above, compressed laterally, with evenly rounded outer margin. Aperture ovate, flattened laterally above periphery, inclined about  $15^\circ$  from shell axis. Parietal barriers 4, extending posteriorly up to  $\frac{3}{16}$  of a whorl, with 1 accessory trace: upper a high, thin blade, extending posteriorly about  $\frac{1}{4}$  whorl, serrated above, a lateral bifidity on posterior 3rd to half of lower side, flat above until anterior 8th to quarter, followed by rapidly increasing descension; 2nd equal in height to 1st, longer anteriorly and posteriorly, broadly expanded above on posterior  $\frac{2}{3}$ , narrowing anteriorly with gradual descension until just before end where descension is very sharp; 3rd equal in height to 2nd, slightly longer, even more broadly expanded above until just before anterior end where abrupt descension occurs, upper edge more strongly reflected upward than in 2nd; 4th very slightly longer than 3rd, only half as high, posterior  $\frac{2}{3}$  with edge broadly expanded and strongly rolled upward, gradually descending anteriorly until just before termination. All parietals with prominent tubercles on expanded upper surfaces and sides of barriers. Accessory trace a very thin, short lamellar blade located just below parietal-palatal margin. Columellar wall with 2 rather low, broadly expanded barriers, lying parallel to plane of coiling, with abrupt anterior descension across columellar callus to lip edge. Palatal barriers 7, extending posteriorly up to more than  $\frac{1}{4}$  whorl, reaching lip edge to slightly recessed, with 3-4 accessory traces above upper palatal: 1st basal in position, posterior half crescentic, weakly expanded and strongly serrated above, next quarter flat, strongly expanded, and a few gross serrations above, abruptly accelerating descension over anterior quarter to lip edge with inward reflection of tip; 2nd through 6th with progressive reduction in height, length, extent of posterior crescentic portion, and degree of anterior expansion above, increasingly with more gradual anterior descension and slightly deeper recession from lip edge; 7th with above trends more pronounced, much smaller than 6th. Accessory traces very short, crescentic to ridgelike blades, expanded above,

deeply recessed, of variable height, situated between upper palatal and parietal-palatal margin.

*Semperdon kororensis* (fig. 98b) has almost the same barrier structure as *S. xyleborus* (fig. 98e), but differs in its closed umbilicus, few and very widely spaced radial ribs, much larger size, and increased whorl count (table LIII). Species of *Aaadonta* differ in their absence of major radial sculpture, generally keeled periphery, and conspicuous swollen beads on the apertural barriers (Solem, 1976b, pp. 467-487, fig. 208b, d-e).

**Description.**—Shell very large, with  $5\frac{1}{4}$  very tightly coiled whorls. Apex flat, whorls of spire descending progressively more rapidly, H/D ratio 0.637. Apical whorls 1%, sculpture of 10 prominent spiral cords. Postnuclear whorls with high, lamellate, slightly protractively sinuated, very widely spaced radial ribs, 25 on the body whorl, whose interstices are 5-8 times their width on spire, becoming more crowded near aperture. Microsculpture a lattice of very fine, moderately widely spaced radial riblets, extremely fine spiral riblets, with a secondary sculpture of more prominent, very crowded spiral cords. Sutures deep, whorls strongly rounded above, somewhat compressed laterally with evenly rounded outer and basal margins. Color light yellowish horn with long, zigzag, reddish flammulations that partially coalesce on shell base. Aperture ovate, somewhat compressed laterally, inclined about  $5^\circ$  from shell axis. Parietal barriers 4, extending  $\frac{1}{8}$ - $\frac{3}{16}$  of a whorl, plus 1 threadlike accessory trace: upper parietal high, bladelike, extending  $\frac{1}{8}$  whorl with gradual anterior descension, not thickened above, posterior half bifid with bifid portion reflected downward; 2nd parietal slightly higher posteriorly, broadly rounded and thickened above; 3rd parietal similar to 2nd but slightly higher and thicker posteriorly, with sharper anterior descension, slightly twisted upward posteriorly; 4th parietal with posterior  $\frac{2}{3}$  broadly expanded above, twisted laterally, anterior half a broad, elevated ridge with nearly vertical anterior descension. Columellar barriers 2: upper a broad, rounded ridge, narrowing to a point and slanting slightly downward across the heavy callus with abrupt anterior descension; 2nd a thinner, higher lamella sinuately twisting across columellar callus. Palatal barriers 7, extending  $\frac{1}{8}$  whorl, upper reduced, 3 accessory traces near top of aperture: 1st through 5th palatals similar in shape, high, crescent-shaped, slightly more highly elevated posteriorly, with progressively more gradual descension toward lip edge; 6th palatal noticeably shortened but only slightly lower; 7th palatal greatly reduced in height and length, lying opposite the 2nd parietal barrier. Accessory palatal traces very short, low, inconspicuous threadlike ridges between 7th palatal and palatal-parietal margin. Height of holotype 3.29 mm., diameter 5.16 mm.

**Holotype.**—Palau Islands: Koror. Collected by Hungerford. BMNH 91.3.17.12.

**Range.**—Koror, Palau Islands.

**Material.**—Koror (1 specimen, BPBM 167441): hillside at Komakan (Station 222), under stones and logs at 100-200 ft. elevation (11 specimens, BPBM 154842-7).

**Remarks.**—The type specimen of *Semperdon kororensis* is by far the most depressed specimen examined, having an H/D ratio of 0.637 compared with a mean of 0.696 for the specimens collected by Kondo. Its depression is approached by a subadult from the Fulton collection (BPBM 167441), with an H/D ratio of 0.645. Quite probably the two unlocalized shells came from another part of the island; quite possibly subspecific separation would be justified when new material is collected. At present only the possibility of local differentiation is noted.



Unquestionably *S. xyleborus* is closely related. They agree in character and in number of major barriers (fig. 98b, e), differing only in *S. xyleborus* usually having two accessory columellar traces and two additional parietal accessory traces located above the upper parietal. *Semperdon kororensis* is altered primarily by closing of the umbilicus and concomitant tightening of the coiling pattern, slightly greater spire protrusion (correlated with the two former changes?), great increase in rib spacing, considerable size enlargement, and, in context of the subfamily, a great change in whorl count (table LIII).

Material of *S. kororensis* was taken only at the one station. Six of 11 (54.5%) shells were adult, an unusually high percentage for a Palau Island species.

*Description of soft parts.*—Available material from adult shells (BPBM 154842) consisted of pallial collars only. Two subadult examples yielded 2 buccal masses and 1 penis. The penis was obviously subadult, with a weak muscle sheath and the total expanded portion about 1 mm. long. Internally the 3 large pilasters were formed, but no details of epiphallal structure could be observed. The epiphallus had the head torn off so that details of vas-epiphallus junction are unknown.

***Semperdon rotanus*, new species. Figures 99d, 100e–f.**

*Diagnosis.*—Shell of average size, diameter 2.48–3.21 mm. (mean 2.95 mm.), with 4–4½ rather tightly coiled whorls. Apex and spire flat or slightly protruding, lower spire descending much more rapidly, body whorl descent greater, spire protrusion less than ¼ body whorl width, H/D ratio 0.452–0.570 (mean 0.518). Apical sculpture of 8–12 (mean 9.9) fine, prominent spiral cords, whose interstices are 2–3 times their width. Postnuclear sculpture of high, narrow, rounded, strongly protractively sinuated radial ribs, 60–95 (mean 76.0) on the body whorl, whose interstices are 3–5 times their width. Ribs/mm. 6.68–9.98 (mean 8.82). Microsculpture of rather prominent radial riblets, 4–9 between each pair of major ribs, crossed by extremely fine and crowded spiral riblets. Weak secondary spiral cording sometimes present on first postapical whorl, never on lower whorls. Umbilicus open, U-shaped, last whorl decoiling more rapidly, contained 3.22–5.25 times (mean 3.92) in the diameter, margins rounded. Sutures deep, whorls with very slight lateral compression above and below rounded periphery, whorl contour almost evenly rounded. Aperture subcircular, moderate lateral compression above periphery in adults, lower margin evenly rounded, inclined about 15° from shell axis. Parietal barriers 3, upper pair high lamellae, lower greatly reduced in size, all extending posteriorly less than ⅓ of a whorl, plus a very fine accessory trace located just below parietal-palatal margin: upper high and crescentic on posterior 3rd, usually slightly expanded, with rather sharp descension to a raised, threadlike anterior 3rd or with more gradual and almost even descension over anterior ⅔; 2nd equal in height on posterior half, flattened or elongately crescentic and weakly expanded above, usually with more gradual descension to threadlike anterior quarter that extends beyond end of upper; 3rd variable, from a low bladelikey ridge to raised thread on posterior half with or rarely without anterior threadlike half to end of 2nd parietal, always less than ½ height of 2nd parietal. Accessory trace a thin, very low, V-shaped or threadlike ridge nearer to parietal-palatal margin than to upper parietal, barely reaching lip edge, often greatly reduced. Columellar wall with 1 (46.5%) or 2 (53.5%) barriers: upper, when present, a low ridge right next to and recessed slightly behind lower, which is a broadly rounded, cordlike ridge, lying parallel to the plane of coiling and reaching just across top of rather heavy columellar callus. Palatal barriers normally 7 (55.0%), often 6 (19.8%), sometimes 8 (14.0%), rarely reduced in number to 4 or 5 (4.2%), rarely increased in number to 9 (5.6%) or 10 (1.4%), short, slightly to moderately recessed, variable in height:

lower at baso-columellar margin, high, crescentic, with abrupt anterior descension almost to edge of callus; 2nd up to twice as high as 1st, length equal to height, with abrupt descension, expanded above and buttressed laterally on callus; 3rd variable in height from size of columellar to ⅔ height of 2nd palatal, if low and ridgelike with abrupt descension, if high, shape as in 2nd palatal; 4th, 5th, and 6th high and crescentic posteriorly, expanded above, with progressively more gradual anterior descension and recession, 6th lower than 2nd, 4th normally slightly lower than 6th, and 5th lower than 4th, but always higher than 3rd; 7th usually greatly reduced in height, elongately crescentic, more deeply recessed, located well above periphery, whereas 6th often located on periphery. Additional trace barriers usually size of 4th or 7th, interspersed between lower barriers, occasionally low and ridgelike, near upper palatal margin. All barriers minutely barbed on top and upper sides.

*Semperdon rotanus* (fig. 99d) is smaller, with fewer whorls, and generally more narrowly umbilicated than *S. heptptychius* (fig. 99a–c). The latter normally has four or five palatals and only rarely (5.7%) six or more palatals; its whorls are noticeably more compressed laterally above and below the rounded periphery. *Semperdon xyleborus* (fig. 98e) has four large parietals, and the seven or eight palatals change size in regular order.

*Description.*—Shell of average size, with slightly more than 4½ relatively tightly coiled whorls. Apex and early spire slightly and evenly elevated, lower spire and body whorl descending much more rapidly, H/D ratio 0.511. Apical whorls 1½, sculpture of 11 narrow, prominent spiral ribs, whose interstices are 2–3 times their width. Postnuclear whorls with protractively sinuated, thin, rounded, relatively crowded radial ribs, 81 on the body whorl, whose interstices are 2–3 times their width. Microsculpture of fine radial riblets, 4–6 between each pair of major ribs, latticed by distinctly lower and much more crowded spiral riblets. Weak secondary spiral cording on first postnuclear whorls, absent on later whorls. Sutures relatively deep, whorls strongly rounded on outer margins, slightly compressed laterally above periphery. Umbilicus U-shaped, decoiling regularly until last whorl, contained 3.68 times in the diameter. Color light yellow-horn with prominent, irregular, sinuated reddish maculation. Aperture circular, slightly compressed laterally above periphery, inclined about 10° from shell axis. Parietal barriers 3, extending posteriorly about ⅓ of a whorl, plus a low, thin lamellar trace between upper parietal and parietal-palatal margin: structure of 1st and 2nd parietals as in diagnosis, with gradual descension to anterior end; 3rd a low ridge, with anterior 3rd threadlike. Columellar wall with single broadly rounded, sharply defined ridge lying parallel to plane of coiling. Palatal barriers 7, typical in shape and size except 1st and 7th larger than usual, plus a very low and short trace between 6th and 7th, then a tubercular trace, deeply recessed, located just below parietal-palatal margin. Height of holotype 1.55 mm., diameter 3.03 mm.

*Holotype.*—Mariana Islands: Rota, Toquan, 400 ft. inland at 20 ft. elevation. Collected July 27, 1925, by H. G. Hornbostel on ferns. BPBM 82477.

*Range.*—Ritidian Point at the northern tip of Guam and Rota Island, Mariana Islands.

*Paratypes.*—Rota (16 specimens, BPBM 82528–30): Toquan, 400 ft. inland at 20 ft. elevation under debris (102 specimens, BPBM 82474–5, BPBM 82477–8, collected July 27, 1925, by H. G. Hornbostel); under stones, 600 yd. inland at 25 ft. elevation, Ugis (18 specimens, BPBM 82002, BPBM 94765, collected July 25, 1925, by H. G. Hornbostel); base of cliff at Lyanggon, under stones 3,000 ft. inland at 20 ft. elevation (6 specimens, BPBM 82416–7, BPBM 82442, collected July 23, 1925, by H. G. Hornbostel);

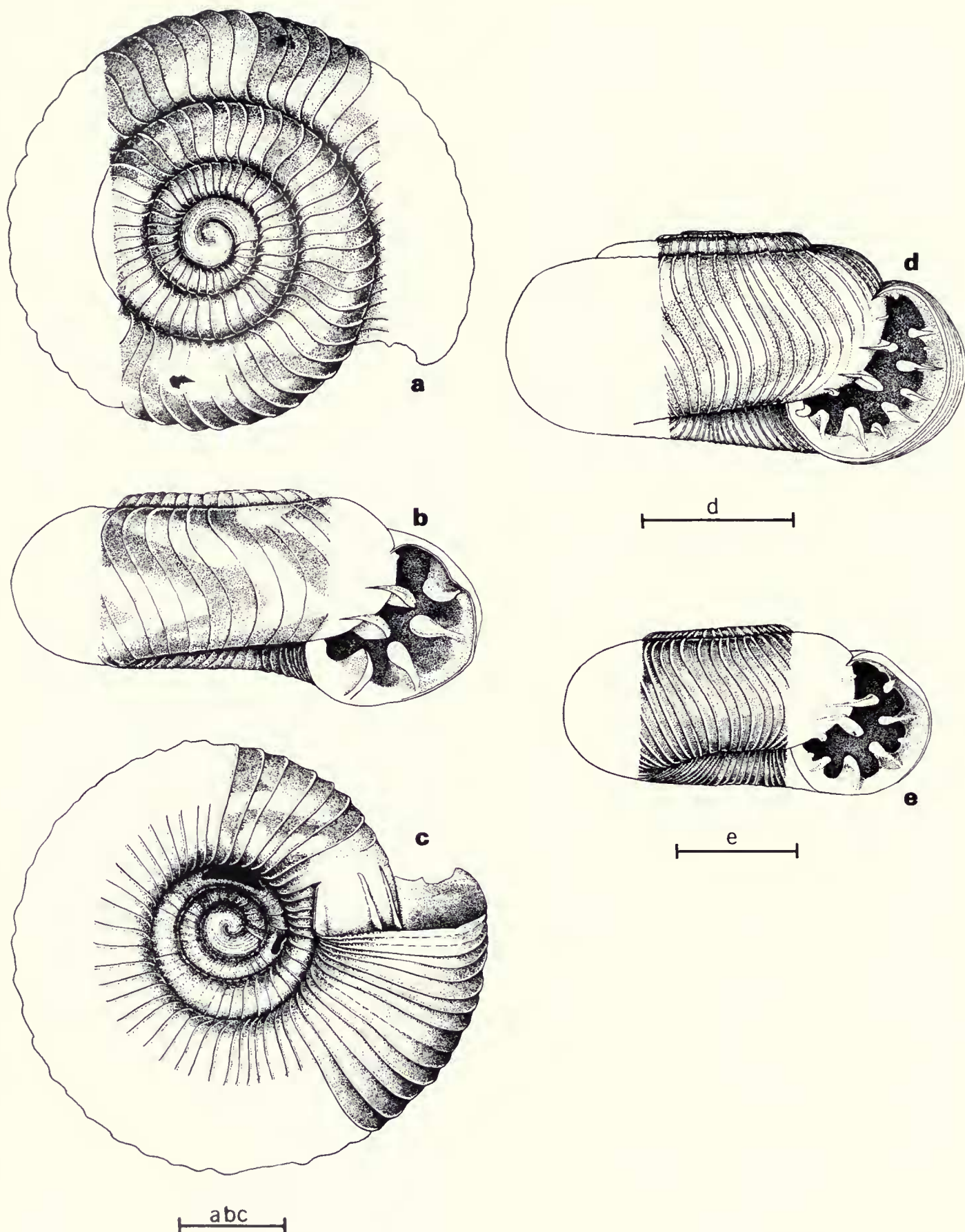


FIG. 99. a-c, e, *Semperdon heptptychius* (Quadras & Möllendorff). Station 134, Mata Cliffs, Talafofo, Guam, Mariana Islands. BPBM 215251; e, 1 mile east of Yigo, Guam. FMNH 24907; d, *Semperdon rotanus*, new species. Toquan, Rota, Mariana Islands. Holotype. BPBM 82477. Scale lines equal 1 mm. (MM).



Muehong, 300 ft. inland at 15 ft. elevation on fern leaves (13 specimens, BPBM 82504–5, collected by H. G. Hornbostel); northwest (Station 40) coast of island on dead wood (36 specimens, BPBM 213218, BPBM 213271, collected May 8–10, 1949, by Y. Kondo); Sabana (Station 83) (6 specimens, collected June 24, 1951, by Y. Kondo).

Guam: Ritidian Point, under stones and logs, tree leaves (2 specimens, BPBM 152752, BPBM 152798, collected April 15–16, 1936, by E. H. Bryan); beach trail and cliffs at 250–535 ft. elevation (Stations 86, 87, 89) at Ritidian Point (4 specimens, BPBM 214438, BPBM 214451, BPBM 214490, collected November 15, 1949, by Y. Kondo); Ritidian (1 specimen, FMNH 28876, collected by H. S. Dybas on May 29, 1945).

**Remarks.**—With the great size and shape variation seen in *Semperdon heptptychius* (tables LVII–LX) and the great barrier number variation found both in that species (table LXIV) and *S. rotanus*, discovery of constant identification features is difficult. *Semperdon heptptychius* could be derived from *S. rotanus* by a slight increase in size, loss of the first, third, and fifth palatals, and development of lateral whorl flattening above the periphery and on the basal margin. The majority of specimens can be separated simply on the basis of palatal barrier count and size, but a very few individuals of *S. rotanus* (5.2%) had only four or five palatals, and a similar proportion of *S. heptptychius* (5.7%) had six to eight palatals (table LXIV). All of these individuals could be allocated on the basis of whorl contour and/or size. In addition, *S. heptptychius* (fig. 99b) has the principal columellar barrier much larger and slanted down from the plane of coiling; *S. rotanus* (fig. 99d) has this much smaller and lying parallel to the plane of coiling.

Samples from local populations on Rota (table LVI) show little significant variation. The shells from Toquan are slightly more widely umbilicated than those from the other stations, but all agree quite well in size and proportions. Ribbing is slightly more crowded in the unlocalized set, but the differences are rather small. Variation in barrier number among adults is larger and is summarized in Table LVII. Generally numbers are too small for meaningful analysis, but recording of this data does suggest areas for further collecting effort.

Specimens from the Ritidian cliff area of Guam are distinctly smaller than the Rota Island specimens, but agree in palatal barriers and whorl contour. The shells are reddish brown in color, whereas all Rota Island examples have a distinct flammulated color pattern. It was not possible to dissect any of these, and reference to *S. rotanus* may have to be changed when soft parts are examined.

One specimen without an exact locality on Rota (BPBM 82528) lacks all apertural barriers. Size, proportions, and sculpture match those of *S. rotanus*, and I have no hesitation in considering this a freak.

Dissection of *S. rotanus* reveals an immediate difference from *S. heptptychius*. The penis (fig. 100e,

P) is proportionately much thicker, and the large bulge of the penis continues below the muscle sheath termination and then narrows abruptly, whereas in *S. heptptychius* (fig. 100b) the penis is slender and tapers gradually after the initial muscle sheath expansion. This difference is caused by the pilaster structure. In *S. heptptychius* there is the typical pattern of many slender longitudinal pilasters that coalesce medially into three very long, bifurcated pilasters that gradually taper into the lower penial tube (fig. 100d); in *S. rotanus* the three major pilasters are very short, perhaps twice as broad as long, and end in a high free tip rather than tapering toward the atrium (fig. 100f). Undoubtedly this is an effective means for reinforcing species separation.

**Description of soft parts.**—Foot and tail about  $\frac{2}{3}$  shell diameter in length. Pedal grooves typical, no marked depression above tail, no caudal horn or middorsal groove present. Gonopore position not noted because of contraction.

Body color yellow-white, a very faint reddish tinge on omatophores and top of head.

Mantle collar thin, rather wide, no glandular extension onto pallial roof. Anus opening alongside external ureteric pore, both just inside pneumostome.

Pallial region extending  $\frac{2}{3}$  whorl apically, agreeing exactly in structure with *Semperdon heptptychius*. Kidney with rectal lobe about 2.0–2.1 mm. long, extending slightly onto parietal wall, pericardial lobes less than half the length. Ureter, heart, principal pulmonary vein, and hindgut as in *S. heptptychius*.

Apical genitalia showing no differences from *S. heptptychius*. Prostate and uterus short, without unusual features.

Vas deferens (fig. 100e, VD) very slender from penioviducal angle to insertion on side of epiphallic head, larger and thin-walled on descending side. Epiphallus (E) much shorter than penis, curved at apex, vas deferens entering laterally on head of epiphallus, further from retractor muscle insertion than in *S. heptptychius* (fig. 100b). Penial retractor (PR) very short, arising from diaphragm, inserting directly into head of epiphallus. Penis (P) about 1.9–2.1 mm. long, expanded head 1.6–1.8 mm. long, with a muscle sheath extending up around epiphallic head as a collar, sheath ending about  $\frac{1}{4}$  of way from head of bulge to sharp constriction of expanded penis portion. Internally (fig. 100f) sheath area with very weak longitudinal pilasters that coalesce and expand into 3 transversely ovate glandular pilasters that cause bulge below end of muscle sheath. Pilasters narrow and tapered at either end, in middle twice as high as long. Atrium (Y) short.

Free oviduct (UV) short, with weak internal pilasters. Spermatheca (S) typical. Vagina (V) tapering gradually to atrium.

Free muscle and digestive systems without unusual features.

(Based on BPBM 82477, adults 3.0–3.2 mm. in diameter, with  $4\frac{1}{4}$ – $4\frac{1}{2}$  whorls.)

***Semperdon heptptychius*** (Quadrass & Möllendorff, 1894). Figures 99a–c, e, 100a–d.

*Endodonta heptptychia* Quadrass & Möllendorff, 1894, Nachr. d. Malak. Gesell., **26** (1–2), p. 15—Mariana Islands.

*Endodonta (Thaumatodon) heptptycha* (sic) Quadrass & Möllendorff, Pilsbry, 1895, Man. Conchol., (2) **9**, p. 339.

*Endodonta (Thaumatodon) tomlini* Gude, 1917, Proc. Malac. Soc. London, **12** (6), p. 317, figs.—Guam, Mariana Islands.

**Diagnosis.**—Shell varying in size from small to large, diameter 2.47–5.17 mm. (mean 3.32 mm.), with  $4\frac{1}{2}$ – $5\frac{1}{2}$  normally to rather tightly coiled whorls. Apex and early spire almost flat to moderately elevated, lower whorls descending moderately to much more rapidly, spire protrusion from  $\frac{1}{5}$  to more than  $\frac{1}{2}$  body whorl width, averaging  $\frac{1}{6}$ , H/D ratio 0.394–0.570 (mean 0.490). Apical sculpture of 8–13 (mean 10.5) fine, prominent spiral cords, whose interstices are about

TABLE LVI. - LOCAL VARIATION IN SEMPERDON ROTANUS.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
<u>Rota Island</u>						
Toquan						
BPBM 82478	6	-----	-----	1.50±0.054 (1.38-1.74)	2.87±0.161 (2.73-3.16)	0.520±0.0100 (0.494-0.552)
BPBM 82477	25	-----	-----	1.58±0.018 (1.36-1.76)	3.03±0.015 (2.88-3.15)	0.520±0.0052 (0.471-0.564)
Muehong						
BPBM 82504	12	70.4±1.66 (60-80)	7.80±0.199 (6.67-8.70)	1.46±0.023 (1.36-1.59)	2.90±0.031 (2.78-3.11)	0.504±0.0043 (0.477-0.535)
Ugis						
BPBM 82002	5	-----	-----	1.57±0.033 (1.48-1.64)	3.00±0.052 (2.89-3.16)	0.524±0.0057 (0.506-0.540)
BPBM 94765	12	75.3±2.89 (66-95)	8.00±0.306 (7.10-9.99)	1.59±0.021 (1.49-1.72)	3.03±0.029 (2.91-3.21)	0.527±0.0043 (0.500-0.552)
Lyanggona						
BPBM 82416,-42	5	-----	-----	1.53±0.076 (1.26-1.69)	2.97±0.054 (2.78-3.08)	0.514±0.0174 (0.452-0.554)
No exact locality						
BPBM 82530	11	82.0±1.89 (75-92)	9.09±0.207 (8.03-9.91)	1.48±0.030 (1.36-1.66)	2.88±0.053 (2.68-3.21)	0.514±0.0069 (0.474-0.563)
<u>Guam Island</u>						
Ritidian Point						
All adults	5	77.6±5.56 (60-90)	9.88±0.643 (8.31-11.48)	1.32±0.052 (1.18-1.48)	2.49±0.052 (2.30-2.60)	0.529±0.0146 (0.487-0.552)

	WHORLS	UMBILICUS	D/U RATIO
<u>Rota</u>			
82478	4 1/4+(4 1/4-4 3/8)	0.77±0.026 (0.66-0.82)	3.75±0.115 (3.45-4.20)
82477	4 3/8+(4 1/8-4 5/8)	0.80±0.011 (0.72-0.89)	3.77±0.046 (3.22-4.18)
82504	4 1/4+(4 1/8-4 1/2)	0.75±0.027 (0.53-0.89)	3.89±0.147 (3.36-5.25)
82002	4 3/8(4 1/8-4 1/2)	0.74±0.017 (0.69-0.79)	4.07±0.052 (3.91-4.19)
84765	4 3/8(4 1/4-4 1/2)	0.75±0.017 (0.69-0.86)	4.03±0.069 (3.62-4.43)
82416	4 1/4-(4-4 3/8)	0.72±0.012 (0.69-0.76)	4.12±0.063 (4.00-4.33)
82530	4 1/4+(4-4 1/2)	0.72±0.022 (0.63-0.86)	4.02±0.078 (3.70-4.50)
<u>Guam</u>			
All	4 1/8+(4-4 3/8)	0.60±0.033 (0.53-0.72)	4.19±0.176 (3.59-4.68)

TABLE LVII. - BARRIER VARIATION IN SEMPERDON ROTANUS.

SET	COLUMELLAR		PALATAL					
	1	2	4	5	6	7	8	9
<u>Toquan</u>								
BPBM 82478	2	4			3	2	1	
BPBM 82477	15	10			2	17	5	1
Muehong	4	8			1	8	2	1
<u>Ugis</u>								
BPBM 82002		5				2	2	1
BPBM 94765	6	6			3	6	1	2
Lyanggona		5			3	2		
No exact locality	2	9	1	1	3	4	1	1
Ritidian Point, Guam	3	2				5		



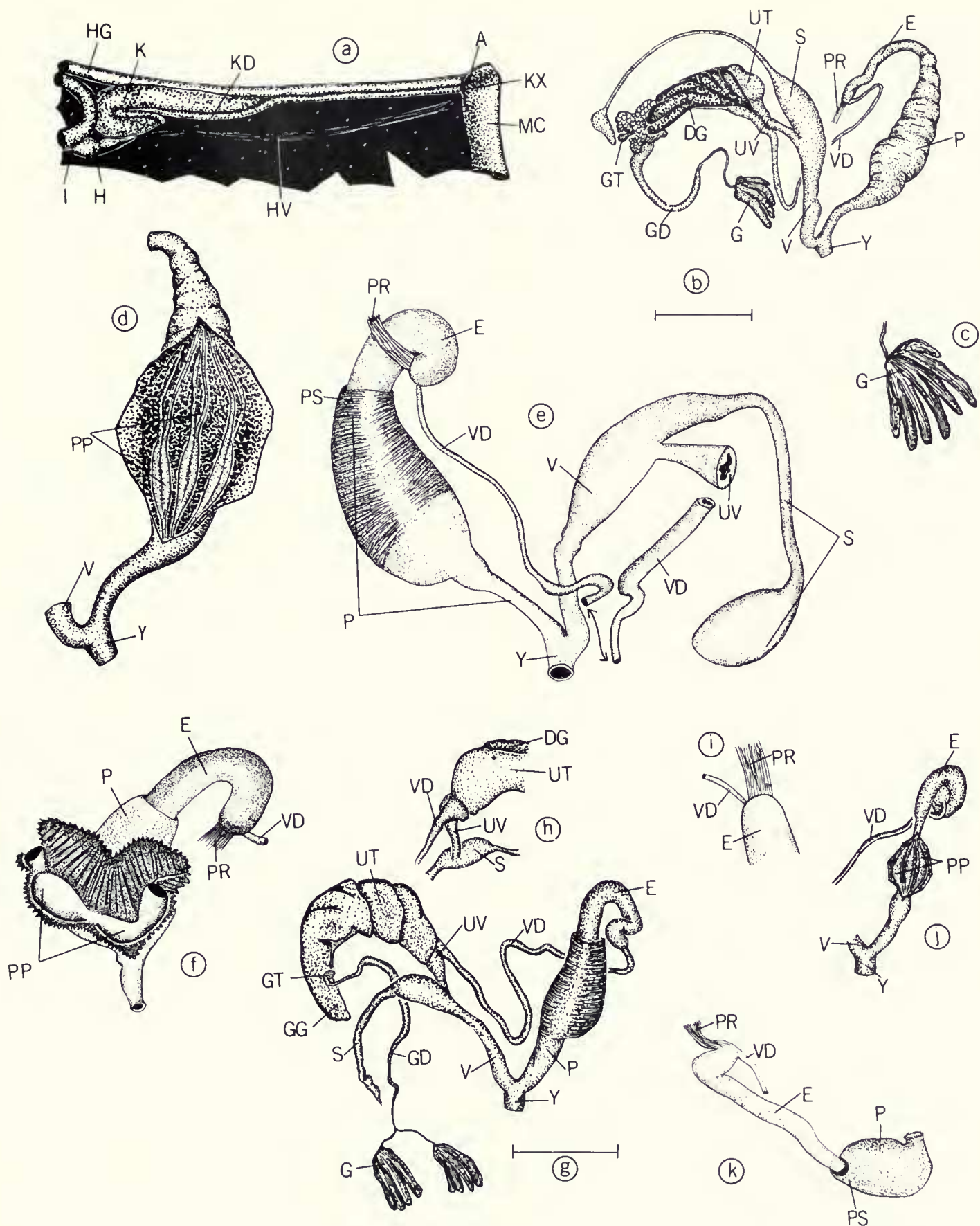


FIG. 100. Anatomy of *Semperdon*: a–d, *Semperdon heptptychius* (Quadras & Möllendorff). Station 74, Alupat, Guam. BPBM 214229. a, pallial region. b, genitalia. c, alveolus of ovotestis. d, interior of penis; e–f, *Semperdon rotanus*. Toquan, Rota. BPBM 82477. e, terminal genitalia. f, interior of penis; g–j, *Semperdon xyleborus*. Station 175, Angaur, Palau. BPBM 158261. g, genitalia. h, detail of vas deferens and free oviduct origin. i, detail of penial retractor and vas deferens insertion on epiphallus. j, interior of penis; k, epiphallus and penis of *Semperdon uncatus*. Station 194, Koror, Palau. BPBM 154850. Scale lines equal 1 mm. (a–d, f–h, j, MO; e, i, k, SH).

3 times their width. Postnuclear sculpture of prominent, rounded, sharply defined widely spaced to crowded, strongly protractively sinuated radial ribs, 35–131 (mean 75.3) on the body whorl, whose interstices are 2–8 times their width. Ribs/mm. 2.97–13.59 (mean 7.84). Microsculpture of rather prominent radial riblets, 2–12 between each pair of major ribs, crossed by much finer and more crowded spiral riblets. Many specimens have weak secondary spiral cording on first postnuclear whorl, but none on lower whorls. Umbilicus narrowly to broadly U-shaped, last whorl decoiling more rapidly, contained 2.69–4.94 times (mean 3.44) in the diameter, margins rounded. Sutures deep, whorls strongly rounded above and on outer margin, distinctly compressed laterally above periphery and on basal margin. Aperture subcircular, compressed laterally above and below rounded periphery, inclined about 15°–30° from shell axis. Parietal wall normally (91.3%) with 3 major barriers extending posteriorly up to  $\frac{3}{16}$  of a whorl, and a superior accessory trace, rarely (3.3%) with trace missing, occasionally (5.1%) with both trace and 3rd parietal absent, very rarely (0.3%) with an additional barrier developed: upper barrier high and crescentic on posterior 3rd, slightly expanded, either with gradual descension to anterior end or with sharper descension to threadlike anterior 3rd; 2nd equal in height, crescentic portion longer and more broadly expanded, anterior descension to raised threadlike quarter extending beyond end of 1st parietal; 3rd varying from a miniature of 1st with anterior  $\frac{3}{4}$  threadlike to a short and deeply recessed cordlike ridge. Accessory trace a very narrow V-shaped to threadlike trace between upper parietal and parietal-palatal margin, reaching only to lip edge. When only first 2 parietals present, both much higher and more broadly expanded. Columellar wall with 1 (42.1%) or 2 (56.4%) barriers: upper, when present, a low, cordlike ridge lying parallel to plane of coiling and reaching top of columellar callus, slightly but distinctly separated from 2nd columellar; 2nd normally a crescentic blade, moderately to broadly rounded above, with gradual descension midway across callus, distinctly angled downward from plane of coiling, rarely (fig. 99b) absent. Rarely (1.2%) with another threadlike trace developed on columellar wall. Palatal barriers short, usually high and crescentic, normally 4 (80.0%), sometimes 5 (13.1%), rarely 6 (3.9%), and very rarely 3 (1.2%), 7 (1.5%), or 8 (0.3%): 1st on basal margin, crescentic, very short, usually bulbously expanded above, with vertical anterior descension almost to lip edge; 2nd very slightly lower or equal in height, on lower palatal wall, pointing toward 2nd parietal, greatly expanded above with more gradual anterior descension; 3rd peripheral in position, equal in height to 2nd, expanded above, with more gradual anterior descension, pointing between 1st and 2nd parietal; 4th supraparietal, much lower and shorter, pointing toward edge of upper parietal, rather deeply recessed, crescentic. Additional palatals located between columellar and 1st palatal or between other pairs of palatals.

*Semperdon heptapychius* (fig. 99a–c, e) normally is separable from *S. rotanus* (fig. 99d) by the presence of only four palatals and much greater lateral compression of the whorls in the former; *S. rotanus* normally has seven palatals and the whorls almost evenly rounded. *Semperdon xyleborus* (fig. 98e) and *S. kororensis* (fig. 98b) have four, instead of three, parietals, and the palatals are much longer and more slender. *Semperdon uncatus* (fig. 97b) has fewer barriers.

*Description.*—Shell moderately large, with slightly less than 4% normally coiled whorls. Apex flattened, lower whorls of spire descending gradually, H/D ratio 0.423. Apical whorls 1%, sculpture of 10 moderately prominent spiral cords. Postnuclear whorls with narrow, prominent, protractively sinuated radial ribs, 67 on the body whorl, whose interstices are 2–5 times their width. Microsculpture of prominent radial riblets crossed by much finer, more closely spaced spiral riblets. Sutures deep, whorls strongly rounded above, slightly flattened laterally above and below rounded periphery. Ground color faint yellowish white with broad, anastomosing reddish brown flammulations becoming slightly lighter in color on shell base. Umbilicus broadly U-shaped, regularly decoiling, widely open, contained

2.70 times in the diameter. Aperture subcircular, compressed laterally above and below periphery, inclined about 15° from shell axis. Parietal barriers 3, plus 1 accessory trace: first 2 coequal, extending about  $\frac{3}{16}$  of a whorl, anterior half a low, narrow ridge, rounded above, posteriorly becoming high and broadly expanded above with rapid posterior descension; lower parietal near columellar margin, low and threadlike anteriorly, becoming bulbously expanded on posterior 3rd. Accessory trace a low threadlike ridge midway between upper parietal margin and 1st parietal. Columellar barrier short, moderately high, crescentic, slanting about 35° from the plane of coiling, with sharp anterior descension, a little recessed from lip margin, with a small, nodular, anterior accessory lamella above. Palatal barriers 4: lower 3 coequal, extending about  $\frac{1}{4}$  whorl, bulbously rounded above, crescent-shaped, high, with gradual anterior descension, located at periphery, palatal-basal margin, and on middle of basal margin; 4th palatal greatly reduced in size, very short, low, bulbously ridgelike, deeply recessed within aperture. Height of lectotype 1.61 mm., diameter 3.82 mm.

*Lectotype of heptapychius.*—Mariana Islands: Guam. Collected by Quadras. SMF 165430; of *tomlini*.—Mariana Islands: Guam. NMW.

*Range.*—Guam, Mariana Islands.

*Paratypes.*—*heptapychius*: SMF 165431, BPBM 86197, BPBM 87460; *tomlini*: NMW, FMNH 46601, FMNH 157481.

*Material.*—Mariana Islands (1 specimen, FMNH 18890): Guam (82 specimens, BPBM 106242, BPBM 167439, BPBM 82710-3, FMNH 18889, FMNH 119305): Tarague (5 specimens, FMNH 46338, FMNH 46347); Tarague Beach area (Station 120) (1 specimen, BPBM 214628); moist limestone forest, 110 m. elevation, Machanao Dist., on tree trunks (1 specimen, BPBM 161460, collected June 16, 1936, by E. H. Bryan); on dead logs (Station 78), near Tailalo, Machanao Dist.,  $2\frac{1}{2}$  miles inland at 500 ft. elevation, on tree trunks and dead logs (110 specimens, BPBM 214313, collected September 13, 1949, by Y. Kondo); under stones in dense forest,  $2\frac{1}{2}$ –3 miles east of Tarague Beach (Station 117), 100–200 yd. inland (4 specimens, BPBM 214554, collected October 14, 1949, by Y. Kondo);  $1\frac{1}{2}$  miles inland, 450 ft. elevation, road from Upi to Salisbury, under stones and on dead leaves (1 specimen, BPBM 153022, collected May 5, 1936, by E. H. Bryan); 1 mile east of Yigo (12 specimens, FMNH 24907, collected by H. S. Dybas on May 26, 1948);  $\frac{1}{2}$  mile inland at 50 ft. elevation, under small stones, Sapon (1 specimen, BPBM 82660, collected October 21, 1925, by H. G. Hornbostel); 2 miles inland at 300 ft. elevation, under stones and logs, Ukudu (58 specimens, BPBM 82737–40, collected November 10, 1925, by Hans G. Hornbostel); under stones and logs, Barrigada, at 500 ft. elevation (17 specimens, BPBM 162078, BPBM 162081–3, collected June 12, 1936, by R. L. Usinger); in coral tombstone, Ypau, north end of Tumon Bay (507 specimens, BPBM 75166–74, collected March 15–17, 1923, by H. G. Hornbostel); Ratilan (7 specimens, FMNH 46348); Oca, north end Alupat Islands (Station 73), Agana Bay, on leaves (2 specimens, BPBM 214203, collected September 10, 1949, by Y. Kondo); Alupat (Station 74) Island, Agana Bay, at 5–20 ft. elevation (54 specimens, BPBM 214229, collected September 11, 1949, by Y. Kondo);



Charlan Trinchera, 300 yd. inland at 70 ft. elevation, under dead breadfruit leaves (177 specimens, BPBM 82612, BPBM 82628–32, BPBM 82646–9, BPBM 82666–72, collected October 21–22, 1925, by H. G. Hornbostel); Aniguat (Station 1), on green leaves (1 specimen, BPBM 212338, collected June 14, 1949, by Y. Kondo); Agana (6 specimens, FMNH 125666); Sinajana-Agana (9 specimens, FMNH 46434); hill behind Asan (Station 43, Commander Marianas Hill) at 500 ft. elevation (5 specimens, BPBM 213327, collected August 5, 1949, by Y. Kondo); Asan Hill (Station 130) at 400 ft. elevation (11 specimens, BPBM 214908, collected October 25, 1949, by Y. Kondo); Pago Bay (26 specimens, USNM 589984, collected August, 1945, by C. S. Richards); under stones and logs, under dead leaves, Mananzana, 2 miles inland at 100 ft. elevation, Yona (3 specimens, BPBM 152959–60, collected April 29, 1936, by E. H. Bryan); under dead leaves, 2½ miles inland at 150 ft. elevation, near Asmadoc Latte, Yona (2 specimens, BPBM 152979, collected April 29, 1936, by E. H. Bryan); Angut (3 specimens, FMNH 57196); on dead leaves in second growth (Station 141) at 700 ft. elevation, Mt. Alifan (1 specimen, BPBM 215124, collected November 2, 1949, by Y. Kondo); on bushes, 1,000 yd. inland at 400 ft. elevation, Talofofo (4 specimens, BPBM 75390, collected June–July, 1923, by H. G. Hornbostel); near Talofofo Cave at 80–90 m. elevation (1 specimen, BPBM 152728, collected April 11, 1936, by E. H. Bryan); Mata Cliffs, between cave and road (Station 134), Talofofo (188 specimens, BPBM 215251, collected October 26, 1949, by Y. Kondo); near summit of Mt. Lamlan (Stations 66, 137) at 1,300–1,334 ft. elevation (9 specimens, BPBM 213417, BPBM 215026, collected September 4 and October 28, 1949, by Y. Kondo); Umatac Spring (Station 123), near metal storage tank (1 specimen, BPBM 214661, collected October 19, 1949, by Y. Kondo).

*Remarks.*—Neither type series was accompanied by an exact locality. Material of *Endodonta heptptychius* (SMF 165431) contained a mixture of sculptural types, ranging from shells with very crowded radial ribbing to very widely spaced ribbing. Probably they represent several populations. Most had normal apertural barriers, but two examples showed the barrier characteristic of *Endodonta tomlini*. The lectotype of *S. heptptychius* is a rather large example with very wide umbilicus, normal barriers, and rather widely spaced radial ribbing. It agrees fairly well with examples taken near Talofofo in southern Guam. Without further fieldwork and dissection of additional material, I believe that designation of a type locality is premature.

*Endodonta tomlini* originally was separated on the basis of having only two parietals and four palatals. Paratype specimens (FMNH 46601, FMNH 157481) are reddish brown dwarfed examples of a variant that occurs in a number of populations and reaches very large size. Although agreeing in having only two parietals, a large umbilicus, large size, and fewer whorls at any given size, they differ greatly in ribbing

pattern (table LVIII). Scattered individuals are known from Tarague in northern Guam (FMNH 46338), Ypau, Tumon Bay (BPBM 75166–7), and Agana (FMNH 125666) in Central Guam, and Station 134, Talofofo (BPBM ex 215251), in southern Guam. I could not dissect this form and do not know whether it is a recurrent mutant for gigantism or represents a relatively rare sympatric species. Probably the name *tomlini* can be applied to this if it is a distinct taxon, even though the types of *tomlini* are small. A few individuals seemed to be transitional between the normal, smaller form with its three parietals plus a trace and this very large form with only two parietals. Most large individuals with normal barriers had 4¾–5 whorls and averaged almost one-half whorl more than examples of the giant form with the same diameter. Study of the problem presented by these individuals would be a good project for a Guam resident.

In general, the “normal” form divides roughly into a widely umbilicated type found in the mountainous areas of southern Guam from Asan to Umatac Spring on the west and Yona and Talofofo on the east, and a more narrowly umbilicated form from the flatter areas of northern Guam from Agana and Barrigada to Tarague Beach and the Machanao district. No material was available from the area on the east coast between Upi, Barrigada, and Agana on one side and Agana, Yona, and Talofofo on the other, from the southeastern tip or from much of the northern area. It is not known whether this is caused by lack of collections or by an absence of the species.

The southern populations conform in general to the type of *S. heptptychius*, although no localized material exactly matches its proportions. Of two collections from Asan Hill, the one from Station 130 (BPBM 214908) is smaller in average size with a moderately widely open umbilicus, whereas a few dead shells from Station 43 (BPBM 213327) are much larger and more widely umbilicated (table LIX). A single adult shell from Yona (BPBM 152959) corresponds closely to the smaller Asan Hill type as does a single shell from Umatac Spring (BPBM 214661). Shells from near the Talofofo Cave are large, with a very widely open umbilicus. They come closest to matching the type specimens in size and umbilical shape but differ in having the radial ribbing more widely spaced. The shells from Mt. Lamlan (Stations 66, 137) are notable primarily for being very dark in color with a moderately open umbilicus. One juvenile shell has six palatal barriers.

In the northern region, shells from Trinchera Beach at Agana are of average size and are relatively depressed in shape with a moderately open umbilicus and rather widely spaced ribbing. Those from Alupat Island at the north end of Agana Bay are dwarfed, slightly more elevated, and with a rather narrow umbilicus. Such small island dwarfing effects are a common phenomenon in land shells and ordinarily have no systematic importance. A few adult shells from Barrigada are large and moderately elevated, with an av-

## SOLEM: ENDODONTOID LAND SNAILS

TABLE LVIII. - LOCAL VARIATION IN TYPES AND LARGE FORM OF SEMPERDON HEPTAPTYCHIUS.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER	H/D RATIO
Types of:						
<u>heptaptychius</u> SMF 165431	11	78.4±9.22 (52-131)	6.42±0.553 (4.93-9.90)	1.82±0.086 (1.51-2.30)	3.93±0.189 (3.29-5.13)	0.462±0.0067 (0.423-0.500)
Types of						
<u>tomlini</u> FMNH 46601, FMNH 157481	2	59.0±8.02 (51-67)	5.43±0.637 (4.79-6.06)	1.60±0.016 (1.58-1.61)	3.45±0.066 (3.39-3.52)	0.463±0.0135 (0.449-0.476)
All of large form	21	69.1 (35-131)	5.47 (2.97-9.90)	1.84 (1.35-2.30)	4.03 (3.39-5.13)	0.455 (0.394-0.500)
Ypau, Tumon Bay BPBM 75166-7	5	40.0±1.87 (35-44)	3.63±0.238 (2.97-4.09)	1.54±0.051 (1.35-1.61)	3.49±0.066 (3.39-3.75)	0.441±0.0148 (0.394-0.476)
Talofofo Sta. 134 ex BPBM 215251	4	57.3±4.13 (51-69)	4.13±0.283 (3.60-4.84)	2.01±0.042 (1.91-2.11)	4.42±0.074 (4.21-4.54)	0.455±0.0106 (0.423-0.469)
Agana FMNH 125666	3	85.3±2.73 (80-89)	6.87±0.113 (6.68-7.07)	1.80±0.055 (1.74-1.91)	3.96±0.1541 (3.72-4.24)	0.456±0.0229 (0.411-0.487)
"Guam" SMF 165436, BPBM 87460	4	123.5±7.52 (116-131)	8.67±1.234 (7.44-9.90)	2.15±0.090 (1.91-2.30)	4.62±0.249 (4.18-5.13)	0.466±0.0116 (0.449-0.500)

	WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS
<u>heptapty.</u>	4 1/2-(4 1/4-4 3/4)	1.26±0.079 (0.95-1.91)	3.16±0.088 (2.69-3.68)	10.7±0.84 (9-12)
<u>tomlini</u>	4+(4-4 1/8)	2.34±0.049 (1.12-1.22)	2.96±0.070 (2.89-3.03)	10.0±1.00 (9-11)
Large form	4 3/8-(4-4 3/4)	1.34 (1.05-1.65)	3.01 (2.69-3.68)	10.2 (9-12)
Ypau	4 3/8(4-1/4-4 1/2)	1.25±0.021 (1.18-1.32)	2.80±0.033 (2.71-2.89)	-----
Talofofo	4 5/8-(4 1/2-4 3/4)	1.48±0.068 (1.32-1.64)	3.00±0.095 (2.74-3.20)	-----
Agana	4 1/4+(4-4 5/8)	1.32±0.114 (1.12-1.51)	3.03±0.153 (2.80-3.32)	-----
"Guam"	4 1/2-(4 1/8-4 3/4)	1.46±0.149 (1.28-1.91)	3.21±0.203 (2.69-3.68)	10.7±0.88 (9-12)

erage umbilicus. Slightly further north at Ukudu the shell is even smaller than the Alupat Island examples, but it is relatively depressed, with a very narrow umbilicus and more crowded ribbing than in the Trinchera Beach material. In the Machanao district at Station 78 near Tailolo a sampled population consists of average size, rather elevated shells with a normal umbilicus but the shells are dark red in color as are the Mt. Lamlan shells. On the northern tip of the island, shells from Tarague Beach are small, rather elevated with a moderately widely open umbilicus, and single specimens from Upi and Tarague are juvenile but with smaller-sized umbilici. Variation in several of these sets is summarized in Table LIX.

Variation in some of the larger, live-collected sets is summarized in Table LIX. Table LVIII summarizes variation in the few sets of the *tomlini* variation. Correlation of these differences with local factors may be possible after considerable fieldwork. For example, sets taken on consecutive days at Trinchera (BPBM 82646 and ex BPBM 82629, on October 21; BPBM 82672, on

October 22) averaged 6.13 ribs/mm. and 4.27 ribs/mm., respectively, yet were not recorded as occupying separate stations. Although most specimens were recorded as being taken under stones, rotting wood, leaves, etc., in dense forest, some examples were taken on tree trunks or leaves in secondary growth, and the largest single collection known came from a tombstone at Ypau. Without knowledge of local environmental factors, interpretation of the variation observed is impossible.

Analysis of ribbing variation (table LXII) in two large and live-collected sets from Machanao (Station 78, BPBM 214313) and Alupat Island (Station 74, BPBM 214229), a large set of dead specimens from Talofofo (Station 134, BPBM 215251), and, for comparison, shells from Ukudu (BPBM 82837) emphasizes the complexity of variation. Frequency distributions (tables LX-LXIII) in diameter, body whorl, rib count, and ribs/mm. indicate considerable variation both within and between populations. The Talofofo set is a thanatocoenosis so that the greater size variation may



TABLE LIX. - LOCAL VARIATION IN *SEMPERDON HEPTAPTYCHIUS*.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM.	HEIGHT	DIAMETER	H/D RATIO
Machanao Sta. 78 BPBM 214313	25	63.0±3.88 (49-84)	6.25±0.324 (5.03-8.12)	1.65±0.022 (1.41-1.88)	3.16±0.021 (2.96-3.45)	0.521±0.0058 (0.467-0.567)
Yigo FMNH 24907	4	73.8±7.32 (58-93)	7.47±0.460 (6.38-8.49)	1.50±0.074 (1.38-1.71)	3.13±0.127 (2.89-3.49)	0.481±0.0094 (0.457-0.500)
Ukudu BPBM 82737-8	12	73.1±2.39 (50-91)	8.44±0.246 (6.05-9.99)	1.34±0.019 (1.23-1.43)	2.81±0.038 (2.55-2.98)	0.476±0.0049 (0.452-0.519)
Barrigada BPBM 162078,-81-3	6	71.7±5.86 (65-76)	6.28±0.175 (5.94-6.51)	1.87±0.065 (1.59-2.02)	3.63±0.080 (3.31-3.84)	0.515±0.0078 (0.480-0.536)
Alupat Sta. 74 BPBM 214229	15	92.1±2.15 (76-128)	10.62±0.206 (8.97-13.59)	1.50±0.023 (1.32-1.66)	2.95±0.032 (2.81-3.28)	0.511±0.0057 (0.465-0.541)
Charlan Trinchera BPBM 82646-9	7	62.7±2.21 (50-70)	6.17±0.207 (5.08-7.19)	1.63±0.042 (1.51-1.84)	3.31±0.032 (3.22-3.32)	0.573±0.0136 (0.455-0.560)
Asan Hill Sta. 130 BPBM 214908	11	-----	-----	1.60±0.033 (1.42-1.79)	3.26±0.052 (2.95-3.48)	0.490±0.0084 (0.436-0.543)
Asan Hill Sta. 43 BPBM 213327	2	70	5.79	1.91±0.132 (1.78-2.04)	3.93±0.082 (3.85-4.01)	0.485±0.024 (0.462-0.508)
Pago Bay USNM 589984	12	62.9±2.05 (53-72)	5.49±0.167 (4.50-6.24)	1.71±0.037 (1.49-1.89)	3.67±0.040 (3.48-3.91)	0.464±0.0078 (0.420-0.514)
Mt. Lamlan Sta. 66,137 BPBM 213417, BPBM 215026	5	85	7.69	1.60±0.029 (1.49-1.66)	3.29±0.068 (3.15-3.54)	0.487±0.0112 (0.458-0.515)

	WHORLS	UMBILICUS	D/U RATIO	APICAL RIBS
Machao.	4 1/2-(4 1/4-4 3/4)	0.90±0.015 (0.76-1.02)	3.52±0.050 (3.03-3.92)	-----
Yigo	4 3/8+(4 1/4-4 1/2)	0.97±0.058 (0.86-1.12)	3.25±0.089 (3.07-3.42)	10.5±0.65 (9-12)
Ukudu	4 1/8-(4-4 1/4)	0.68±0.023 (0.56-0.82)	4.13±0.118 (3.44-4.94)	9
Barrig.	4 1/2+(4 1/4-4 7/8)	1.01±0.037 (0.86-1.12)	3.59±0.143 (3.24-4.23)	11.5±0.65 (10-13)
Alupat	4 1/8+(4-4 1/2)	0.77±0.016 (0.66-0.99)	3.82±0.072 (3.36-4.47)	-----
Charlan	4 3/8+(4 1/4-4 1/2)	0.94±0.026 (0.82-1.02)	3.54±0.096 (3.33-4.04)	10.8±0.54 (9-13)
Asan 130	4 3/8(4 1/4-4 5/8)	0.99±0.026 (0.86-1.12)	3.28±0.054 (2.97-3.54)	-----
Asan 43	5-(4 3/4-5 1/8)	1.40±0.017 (1.38-1.41)	2.83±0.025 (2.79-2.84)	-----
Pago	4 5/8+(4 1/2-4 3/4)	1.25±0.025 (1.15-1.41)	2.93±0.040 (2.72-3.17)	-----
Lamlan	4 1/4(4 1/8-4 1/2)	1.03±0.040 (0.89-1.12)	3.18±0.098 (2.94-3.52)	-----

reflect temporal variations. Barrier variation in the Alupat and Machanao sets (table LXIV) indicates the existence of local variation in both columellar and palatal barriers. The Talofofa set had the apertures clogged with dirt, and it was not practical to clean and check so many specimens.

Apparently *Semperdon heptptychius* still could be collected in quantity on Guam. Studies of local variation in relation to forest disturbance and moisture relationships might yield very important data and would be very suitable projects for local students.

*Description of soft parts.*—Foot and tail about 1.8–2.0 mm. long when extended, truncated anteriorly, slightly tapering posteriorly.

Pedal grooves high on sides of foot, meeting over tail with suprapedal weaker, no caudal horn or middorsal groove developed. Slime network indistinct. Head and ommatophores without unusual features. Gonopore position not seen because of partial contraction. Body color yellow-white, ommatophores grayish red, a very slight gray speckling on back of head.

Mantle collar (MC) thick and wide, no obvious glandular extension onto pallial roof. Anus (A) open next to external ureteric pore just inside pneumostome.

Pallial region (fig. 100a) extending apically  $\frac{2}{3}$  of a whorl. Lung roof clear, no glandular extension or speckling. Kidney (K) bilobed, rectal lobe about 2.0 mm. long, more than twice length of pericardial, crossing hindgut and extending onto parietal wall for much of length. Pericardial arm equal in length to heart. Ureter (KD) with arms tightly compacted between kidney lobes. Heart (H) angled from hindgut. Principal pulmonary vein (HV) not branched, rather prom-

TABLE LX. - SCULPTURE VARIATION IN SEMPERDON HEPTAPTYCHIUS.

	Talofofo (BPBM 215251)	Machanao (BPBM 214313)	Alupat (BPBM 214229)	Ukudu (BPBM 82837)
Ribs	65.1±0.93 (46-92)	88.6±1.22 (65-111)	91.7±2.08 (72-128)	75.7±2.56 (66-91)
Ribs/mm.	6.51±0.083 (4.72-9.34)	9.57±0.125 (7.01-12.9)	10.6±0.213 (8.15-13.6)	8.77±0.233 (7.76-9.99)
Diameter	3.18±0.021 (2.76-3.65)	2.94±0.017 (2.58-3.42)	2.75±0.020 (2.55-3.00)	2.74±0.034 (2.61-2.90)
Number of Specimens	111	110	28	9

TABLE LXI. - FREQUENCY DISTRIBUTION OF DIAMETER IN  
POPULATIONS OF SEMPERDON HEPTAPTYCHIUS.

Diameter in mm.	Talofofo (BPBM 215251)	Machanao (BPBM 214313)	Alupat (BPBM 214229)
2.55-2.62		3	3
2.63-2.70		4	7
2.71-2.78	1	13	9
2.79-2.86	5	13	6
2.87-2.94	16	16	1
2.95-3.02	9	20	2
3.03-3.10	11	20	
3.11-3.18	14	8	
3.19-3.26	15	8	
3.27-3.34	13	2	
3.35-3.42	7	3	
3.43-3.50	8		
3.51-3.58	10		
3.59-3.66	2		

TABLE LXII. - FREQUENCY DISTRIBUTION OF RIBS IN POPULATIONS  
OF SEMPERDON HEPTAPTYCHIUS.

Number of ribs	Talofofo (BPBM 215251)	Machanao (BPBM 214313)	Alupat (BPBM 214229)
45-49	3	1	
50-54	9	1	
55-59	24	1	
60-64	22	1	
65-69	21	7	
70-74	12	6	1
75-79	8	11	1
80-84	8	16	4
85-89	3	20	7
90-94	1	15	7
95-99		16	4
100-104		10	2
105-109			
110-114		4	1
115-119			
120-124		1	
125-129			1

TABLE LXIII. - FREQUENCY DISTRIBUTION OF RIBS/MM. IN  
POPULATIONS OF SEMPERDON HEPTAPTYCHIUS.

Ribs/mm.	Talofofo (BPBM 215251)	Machanao (BPBM 214313)	Alupat (BPBM 214229)
4.6-5.3	8	2	
5.4-6.5	57	5	
6.6-7.3	29	1	
7.4-8.1	13	9	1
8.2-8.9	2	19	1
9.0-9.7	2	33	4
9.8-10.5		29	9
10.6-11.3		7	7
11.4-12.1		4	3
12.2-12.9		1	2
13.0-13.7			1



TABLE LXIV. — BARRIER VARIATION IN  
SEMPERDON HEPTAPTYCHIUS.

	Machanao (BPBM 214313)	Alupat (BPBM 214229)
Parietals		
2		1
3	5	3
4	98	45
5		1
Columellars		
1	12	20
2	89	28
3	2	2
Palatals		
4	67	40
5	24	6
6	9	2
7	3	1
8		1

inent. Hindgut (HG) continuing apicad of kidney base for  $\frac{1}{16}$  of a whorl, intestinal loops typical.

Ovotestis (fig. 100b–c, G) a single clump of palmately clavate alveoli located above stomach margin. Hermaphroditic duct (G) iridescent, narrow, uncoiled to partly kinked near anterior end. Albumen gland (GG) short and compact, acini small. Talon (GT) and carrefour buried in albumen gland, junction as in *Ladronellum mariannarum* (fig. 102e). Prostate (DG) short with a few very large acini opening into groove on inner surface of uterine wall. Uterus (UT) bipartite, lower expanded chamber complexly folded.

Vas deferens (VD) thick and thin-walled to penioviducal angle, reflexing as a very slender muscular tube to insert on head of epiphallus at side of penial retractor insertion. Epiphallus (E) a slender, coiled tube, shorter than penis, with internal longitudinal pilasters, narrowing after entering extended penial sheath collar before epiphallic pore. Penial retractor (PR) short, arising from diaphragm, inserting directly onto head of epiphallus to side of vas deferens entrance. Penis (P) about 2.0–2.2 mm. long, slender, upper  $\frac{1}{2}$ – $\frac{3}{4}$  with muscle sheath that extends 2.0 mm. beyond epiphallus, lower portion a tapering thin-walled tube. Muscle sheath heavy, penis internally (fig. 100d) with very fine pilasters radiating from epiphallic pore, coalescing about middle of muscle sheath area into 3 thicker, bifurcated pilasters that taper into glandular walls of lower tube. Atrium (Y) short.

Free oviduct (UV) short, narrow. Spermatheca (S) with elongated head lying slightly above albumen gland, shaft very slender to level of free oviduct, rapidly and grossly expanded with complex internal pilasters. Vagina (V) long, tapering gradually to atrium with progressively smaller internal pilasters.

Free muscle system typical.

(Based on BPBM 214229, several whole individuals, 2.7–2.8 mm. in diameter with  $\frac{4}{5}$ – $\frac{4}{4}$  whorls, and extracted fragments.)

### Genus *Ladronellum*, new genus

Shell large, averaging  $\frac{4}{5}$  rather tightly coiled whorls. Apex and spire strongly elevated, last whorl descending more rapidly, spire

protrusion about  $\frac{1}{5}$  body whorl width. Apical sculpture of fine widely spaced spiral cords. Postnuclear whorls with high, prominent protractively sinuated, widely spaced radial ribs, averaging 52 on the body whorl. Microsculpture of coequal radial and spiral riblets, no secondary spiral cording. Umbilicus open, V-shaped, regularly decoiling. Sutures deep, whorls strongly and evenly rounded. Aperture circular, inclined about 20° from shell axis. Parietal wall with single, recessed, small barrier. Columellar and palatal wall each with single very small barrier. Pallial region with rectal kidney lobe longer than pericardial, latter narrowed. Apical and midvisceral genitalia without unusual features. Vas deferens as in *Himeroconcha*, inserting laterally below penial retractor insertion on head of epiphallus. Penis with sheath forming an epiphallic collar, internally with many narrow pilasters radiating from epiphallic pore, uniting to form single huge inflatable pilaster occupying lower  $\frac{2}{3}$  of penis. Vagina with lower portion very long and slender, spermatheca typical.

*Type species.*—*Endodonta mariannarum* Quadras & Möllendorff, 1894.

Total lack of secondary spiral cording, presence of three small apertural barriers, the much higher spire, and great alteration of the penial pilaster pattern are the significant characters separating *Ladronellum* from the otherwise similar appearing, but barrier-free, *Himeroconcha*. More detailed comparisons are given in the discussion of Semperdoninae on p. 236.

The single species has been collected at scattered localities on Guam. It is much darker in shell color than any other Mariana Islands charopid.

The name *Ladronellum* is freely adapted from the old Spanish names for the islands.

***Ladronellum mariannarum*** (Quadras & Möllendorff, 1894). Figures 101a–c, 102a–f.

*Endodonta mariannarum* Quadras & Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), pp. 14–15—Mariana Islands.

*Endodonta (Thaumatodon) mariannarum* Quadras & Möllendorff, Pilsbry, 1895, Man. Conchol., (2) 9, p. 339.

*Diagnosis.*—Shell larger than average, diameter 3.03–4.28 mm. (mean 3.66 mm.), with  $\frac{4}{5}$ – $\frac{5}{5}$  rather tightly coiled whorls. Apex and spire strongly and almost evenly elevated, body whorl descending more rapidly, spire protrusion about  $\frac{1}{5}$  body whorl width, H/D ratio 0.590–0.780 (mean 0.652). Apical sculpture of 9–13 (mean 10.5) fine spiral cords whose interstices are 3–4 times their width. Postnuclear sculpture of high, rounded, prominent, protractively sinuated radial ribs, 46–62 (mean 51.8) on the body whorl, whose interstices are about 4–7 times their width. Microsculpture under 96× magnification appearing to be a lattice of coequal radial and spiral riblets, no trace of distinct secondary spiral cording. Umbilicus V-shaped, regularly decoiling, contained 3.24–4.76 times (mean 3.77) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above with evenly rounded outer margins. Aperture circular, becoming slightly constricted and flattened laterally above periphery in gerontic specimens, inclined about 20° from shell axis. Parietal wall with single moderately recessed, short, low, and elongately crescentic to high and crescentic barrier, normally slightly expanded above and extending posteriorly about  $\frac{1}{5}$  whorl. Columellar wall with broadly rounded, low crescentic to crescentic, short barrier located just above baso-columellar margin, reaching top of weak columellar callus and extending less than  $\frac{1}{5}$  whorl posteriorly, rarely absent. Palatal wall with single very weak V-shaped to low lamellar or crescentic ridge located below periphery, moderately recessed, extending about  $\frac{1}{5}$  whorl posteriorly, rarely absent.

The higher spire, absence of distinct secondary spiral cording, evenly rounded periphery, and presence of weak apertural barriers immediately separate *Ladronellum mariannarum* (fig. 101a–c) from any

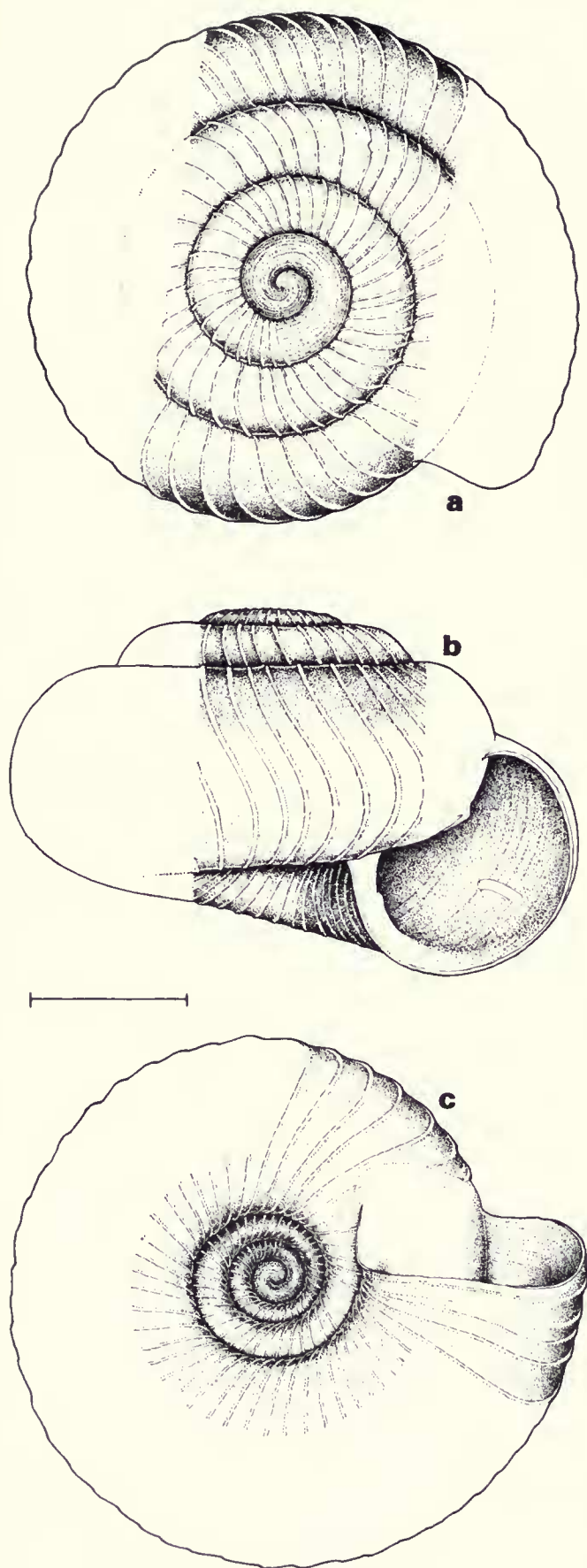


FIG. 101. a-c, *Ladronellum mariannarum* (Quadras & Möllendorff). Station 137, Mt. Lamalan, Guam, Mariana Islands. BPBM 215029. Scale line equals 1 mm. (MM).

*Himeroconcha* (figs. 104–105). The Mariana *Semperdon* (fig. 99a–e) have many more apertural barriers.

*Description*.—Shell relatively large, with 4¼ moderately tightly coiled whorls. Apex and spire strongly and evenly elevated, body whorl descending more rapidly, H/D ratio 0.654. Apical whorls 1½, sculpture of 12 narrow but prominent spiral ribs with faint indications of radial microsculpture near end. Postnuclear whorls with prominent, rounded, somewhat protractively sinuated radial ribs, 46 on the body whorl, whose interstices are 4–6 times their width. Microsculpture a lattice of coequal radial and spiral riblets. Sutures moderately impressed, whorls strongly rounded above without distinct flattening. Color purplish reddish brown on later whorls, apex light yellow-horn. Umbilicus narrowly V-shaped, regularly decoiling, contained 3.82 times in the diameter. Aperture circular, very slightly flattened laterally and on basal margin, inclined about 10° from shell axis, with relatively sinuated lip. Parietal wall with single centrally placed barrier, moderately recessed, extending about ⅓ whorl, broadly rounded, with equal anterior descension and posterior rise. Columellar wall with single, very short, globosely crescentic barrier, moderately recessed within aperture. Palatal wall with single subperipheral, low, broadly rounded ridge extending less than ⅓ whorl, rather deeply recessed within aperture. Barriers minutely pustulose above. Height of lectotype 2.30 mm., diameter 3.65 mm.

*Lectotype*.—Mariana Islands: Guam. Collected by Quadras. SMF 165730.

*Range*.—Guam, Mariana Islands.

*Paratypes*.—SMF 165731, BPBM 86196, BPBM 87461.

*Material*.—Guam (2 specimens, BPBM 167440): Agut (6 specimens, FMNH 46253); Mt. Lamalan (Stations 66, 137) at 1,300–1,334 ft. elevation (127 specimens, BPBM 213414–6, BPBM 215027–30); Mt. Alifan (Station 142) at 800 ft. elevation (2 specimens, BPBM 215136); Talofofo (Station 134), between cave and road (5 specimens, BPBM 215252).

*Remarks*.—Specimens of *Ladronellum mariannarum* were collected at Station 66 on Mt. Lamalan on September 4, 1949, and at Station 137 on October 28, 1949, by Yoshio Kondo and colleagues. Despite the stations being located only a short distance apart, there are gross size differences between the populations. Those from Station 66 agree in size and shape with the types and a set from “Agut” (table LXV), but specimens from Station 137 are substantially larger in size. They average 0.32 whorls more, 0.66 mm. more in diameter, are somewhat more widely umbilicated, and have more major radial ribs. The latter difference correlates with the change in diameter, because the rib spacing, as indicated by ribs/mm., is identical. Station 66 was indicated as containing “open forest,” whereas Station 137 was characterized as “open and dense forest.” Two-thirds (10 of 15) of the Station 66 shells were adult, but only 22.3% (25 of 112) from Station 137. The time span and adult ratios are not compatible with seasonality. Fieldwork to investigate the habitat differences and nature of the size change would be desirable. I suspect that this is a semiariboreal species and thus is more apt to show ecophenotypic variations. Only one shell from Station 142 was adult; all the Talofofo shells were juvenile.

Differences from other Mariana Island species are covered in the diagnosis above. In color and general



TABLE LXV. - LOCAL VARIATION IN LADRONELLUM AND HIMEROCONCHA.

	NUMBER OF SPECIMENS	RIBS	RIBS/MM	HEIGHT	DIAMETER	H/D RATIO
<u>Ladronellum</u>						
<u>mariannarum</u>						
Sta. 66 BPBM 213414-5	10	49.6±1.49 (46-57)	4.41±0.116 (4.50-5.61)	2.24±0.033 (2.05-2.35)	3.35±0.044 (3.05-3.54)	0.667±0.0076 (0.643-0.710)
Sta. 137 BPBM 215027-8	25	57.0±2.89 (52-62)	4.40±0.125 (4.19-4.62)	2.62±0.029 (2.38-2.95)	4.01±0.028 (3.77-4.30)	0.654±0.0082 (0.590-0.780)
Agut FMNH 46253	6	-----	-----	2.03±0.038 (1.91-2.17)	3.21±0.051 (3.06-3.39)	0.633±0.0100 (0.606-0.667)
TYPES: SMF 165730-1	6	48.3±1.20 (46-50)	4.44±0.157 (4.15-4.69)	2.25±0.034 (2.11-2.34)	3.38±0.044 (3.22-3.52)	0.666±0.0088 (0.646-0.703)
<u>Himeroconcha</u>						
<u>fusca</u>						
Sta. 137 BPBM 215020	12	-----	-----	3.03±0.057 (2.75-3.33)	6.35±0.107 (5.75-6.67)	0.479±0.0126 (0.411-0.550)
		WHORLS	UMBILICUS	D/U RATIO	APICAL CORDS	
<u>Ladronellum</u>						
<u>mariannarum</u>						
Sta. 66	4	1/2+(4 1/4-5)	0.91±0.021 (0.82-1.02)	3.95±0.111 (3.61-4.76)	11.0±0.51 (9-12)	
Sta. 137	4	7/8-(4 1/2-5 1/8)	1.10±0.016 (0.95-1.25)	3.65±0.042 (3.24-3.94)	10.5±0.50 (10-11)	
Agut	4	3/8+(4 1/4-4 1/2)	0.80±0.044 (0.69-0.95)	4.08±0.192 (3.55-4.76)	10.8±0.48 (9-12)	
Types	4	1/2+(4 3/8-4 3/4)	0.84±0.039 (0.69-0.95)	4.07±0.154 (3.66-4.76)	12	
<u>Himeroconcha</u>						
<u>fusca</u>						
Sta. 137	4	1/2-(4 1/4-4 3/4)	1.43±0.052 (1.18-1.70)	4.48±0.114 (4.00-5.10)	-----	

sculptural appearance this species seems closely related to *Himeroconcha rotula* (fig. 104a-c). The latter has very prominent secondary spiral cording, a much lower spire, no apertural denticles, and the anatomy is distinctly different. *Ladronellum* has the most modified penis in the epiphallate Micronesian complex. All other species have modified versions of three pilasters within the penial sheath zone or just below it, whereas *Ladronellum* (fig. 102d) has a single huge pilaster that extends from the penis apex to the atrium. The extent to which the long vagina with suddenly expanded upper vaginal shaft correlates with the functioning of this pilaster is unknown. It contrasts with the generally shorter and more gradually tapering vaginae in the sympatric *Himeroconcha* (fig. 103b, f) and *Semperdon* (fig. 100d) of Mt. Lamlan. Penial diameter varied tremendously in dissected material. I suspect that this results from differential reaction during drowning. In some the penial pilaster was grossly enlarged, in others it was collapsed into a wrinkled sac as illustrated (fig. 102d). The pilaster is roughly U-shaped, with one arm extending further apically and much larger in size, in some expanded at upper tip and flanking the vas deferens pore, in others not as large or as long. Particularly in expanded examples, the lower tip

of the pilaster extends below the vaginal entrance and partway into the atrium.

Apertural barriers are highly variable in size and shape, with one or two examples having no trace of the columellar and about eight specimens having a barely detectable trace or lacking the palatal barrier. Barrier form can be derived from the *Semperdon* pattern, and I am certain these are vestigial in *Ladronellum*.

*Description of soft parts.*—Foot and tail about equal to shell diameter, truncated anteriorly, very slightly tapering, and broadly rounded posteriorly. Sole undivided, pedal grooves quite high on foot, suprapedal much weaker, both uniting over tail without marked depressions, no caudal horn or middorsal groove present. Slime network prominent, on tail transverse. Head and ommatophores typical. Gonopore located midway between and slightly behind bases of right ommatophore and right rhinophore.

Body color light yellow-white on foot sides and tail, light gray tone on back of head and edge of mantle collar.

Mantle collar (MC) broad, thin edge reflected and curled in preserved material, some indication of glandular extension onto pallial roof. Pneumostome with a slight right mantle lobe reflection permitting partial to complete closure. Anus (A) opening in pneumostome, slightly posterior to external ureteric pore (KX).

Pallial region (fig. 102c) extending apically about ¾ of a whorl or slightly less, length dependent on degree of contraction. Lung roof clear, without granulations or darker markings. Kidney (K) with rectal lobes about 2.1 mm. long, crossing hindgut and extending onto

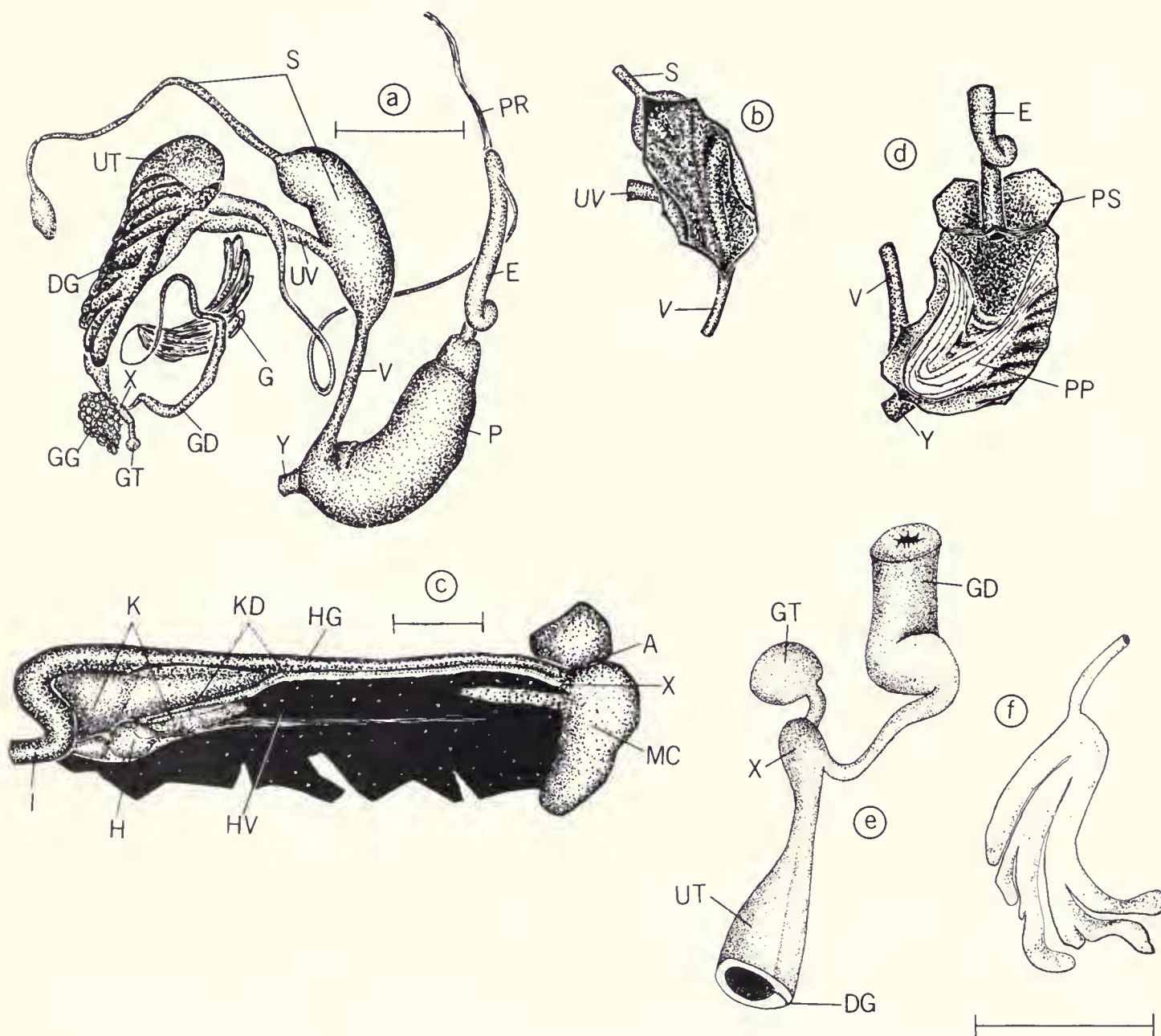


FIG. 102. Anatomy of *Ladronellum mariannarum* (Quadras & Möllendorff). Station 137, Mt. Lamalan, Guam. BPBM 215028: a, genitalia; b, interior of spermathecal shaft base and upper vagina; c, pallial region; d, interior of penis; e, detail of carrefour region; f, compound alveolus of ovotestis. Scale lines equal 1 mm. (a-d, MO; e-f, SH).

parietal wall, thick in middle, strongly tapered posteriorly, pericardial lobe about 1.8 mm. long, distinctly shorter and narrower than rectal lobe. Base of kidney square, lying above intestinal loops. Ureter (KD) with primary and first part of secondary arms tightly compacted between kidney lobes and narrow, anterior part of secondary ureter almost equal to hindgut in diameter. Heart (H) less than  $\frac{1}{2}$  length pericardial kidney lobe, slightly angled from hindgut. Principal pulmonary vein (HV) simple, unbranched, not clearly defined on lung surface. Hindgut (HG) deflecting downward at kidney base, intestinal looping tightly and narrowly coiled.

Ovotestis (fig. 102a, G) separated from stomach apex by narrow strip of digestive gland, extending apically  $\frac{1}{2}$  whorl, composed of a single clump of iridescent, palmately clavate alveoli (fig. 102f), variable in length and splitting. Hermaphroditic duct (G) a greenish iridescent tube of variable diameter, not coiled or kinked, largest just before abrupt narrowing to reflex up to junction with carrefour. Albumen gland (GG) very small, compact, lying next to intestinal loops

above pallial cavity apex, acini rather small. Talon (GT) buried in albumen gland, globular head followed by a short shaft leading to expanded carrefour. Details of talon-carrefour area (fig. 102e) quite clear. Prostate (DG) a single row of very large acini opening into groove on inner wall of uterine chamber, at apex prostatic walls thicker than uterine, ratio changing after start of expanded uterine chamber. Uterus (UT) bipartite, lower chamber grossly expanded, walls much thicker and with weak internal pilasters.

Vas deferens (VD) thick at first, thin-walled, tapering to a very slender muscular tube by end of free oviduct, reflexing at penioviducal angle toward epiphallus, not bound to surface of penis. Epiphallus (E) a long double tube, vas deferens entering laterally about 0.2 mm. below head. Shaft of epiphallus entering penial sheath. Penial retractor (PR) equal in length to epiphallus, arising from diaphragm, inserting on head of epiphallus. Penis (P) about 1.6–2.0 mm. long, a muscular sheath collar extending up around base of epiphallus. Latter opening by a simple pore with numerous



very narrow longitudinal pilasters (not shown in fig. 102d) radiating down walls to start of huge horseshoe-shaped pilaster (PP) that occupies most of penis chamber. Pilaster slightly to grossly swollen in dissected material, slightly expanded individual figured. Atrium (Y) short and very narrow.

Free oviduct (UV) short and slender, scarcely larger in diameter than first part of vas deferens. Joins with spermatheca to form vagina, but spermathecal expansion continues beyond junction with free oviduct. Spermatheca (S) with small oval head next to albumen gland, shaft very slender to base of uterus, then grossly expanded with thick glandular walls forming indistinct pilasters. Vagina (V) starts as a groove along basal part of spermathecal expansion, equal in length to or slightly longer than penis.

Free muscle system without unusual features. Right omatophoral retractor passing through penioviducal angle, joining right rhinophoral retractor. Tentacular retractors unite with tail fan and buccal retractor to form columellar muscle. Buccal retractors not split, inserting slightly behind middle of buccal mass in U-shaped fan, arising from columellar muscle. Esophagus slender, typical. Stomach occupying slightly less than one whorl, filling entire parietal and most of palatal walls, initial expansion very rapid, tapering rapidly at apex to intestinal reflexion. Intestine following basal margin of whorl to base of kidney, up and backward, then forward as hindgut. Salivary glands joined above esophagus on posterior half.

(Based on BPBM 215028, adult specimens, 3.78–3.88 mm. in diameter, with 4½–4¾ whorls.)

### Genus *Himeroconcha*, new genus

Shell moderately to extremely large, with 4¼–4½ normally coiled whorls, reduced to 3½ loosely coiled whorls in *lamlanensis*, body whorl descending more rapidly. Apical sculpture averaging 7.5–10 prominent spiral cords, reduced in *lamlanensis*, larger species with increasing intrusion of radial elements. Postnuclear sculpture of low, irregular, protractively sinuated radial ribs, greatly reduced in larger species. Microsculpture of very fine microreticulations visible between very prominent secondary spiral cords, reduced in *lamlanensis*. Umbilicus rather widely open, U- to V-shaped, regularly decoiling, margins rounded. Sutures deep to shallow, whorls with periphery rounded (*lamlanensis*, *rotula*) to angulated and protruded (*quadrasi*, *fusca*). Aperture without barriers. Pallial region as in *Ladronellum*, with kidney lobes equal or pericardial slightly shorter, usually pericardial much narrower than rectal. Apical and midvisceral genitalia without unusual features. Vas deferens thin-walled and tapering to penioviducal angle, then very slender and muscular, entering slightly below head on side of epiphallus. Basal part of epiphallus surrounded by collar from penial sheath, opening into penis through simple pore. Penis short to long, tapering to bulging, internally with apical portion smooth (*rotula*) or with many longitudinal weak pilasters that fuse into 3 large pilasters after a short (*fusca*) to longer (*rotula*, *lamlanensis*) distance from apex. Size of pilasters variable. Relative sizes and proportions of spermathecal expansion and vaginal tract variable.

*Type species.*—*Patula fusca* Quadras & Möllendorff, 1894.

Except for the Tongan *Tuimalila* (fig. 78a–f) and the Fijian subfossil *Lauopa* (fig. 77a–c), species of *Himeroconcha* (figs. 104–105) are the largest Pacific Island Charopidae. Although the endodontid genera *Nesodiscus*, *Libera*, *Endodonta*, *Pseudolibera*, *Nesophila*, and *Gambiodonta* exceed this size range (Solem, 1976b), the vast majority of species are much smaller.

Four species of *Himeroconcha* are known from Guam. Possibly additional taxa can be found on Saipan, but it is doubtful that the genus had an extensive range. Although only two species, *H. lamlanensis*

and *H. fusca*, have been collected together so far, dissection suggests that a greater degree of sympatry prevails (or prevailed) under undisturbed conditions. Although the penis size in the two species is actually and proportionately disparate, 2.0 mm. long (51% of shell diameter) in *lamlanensis* and 2.7 mm. long (44% of shell diameter) in *fusca*, the latter (fig. 103f) has the major pilasters forming just below the epiphallallic pore, whereas in *H. lamlanensis* (fig. 103b) they form about halfway from the pore to the atrium. The effective pilaster length of about 1.35 mm. in *H. fusca* contrasts with an effective pilaster length of about 0.75 mm. in *H. lamlanensis*. Although the penis of *H. fusca* is only about 35% longer, the stimulatory length is 80% longer. Undoubtedly this proportionately greater change serves to enforce species recognition. The single example of *H. rotula* has a shorter, 1.6 mm. long, penis with *H. lamlanensis*-type pilasters, but lacks the fine upper pilasters seen in all other Micronesian epiphallate species. It has the vaginal region (fig. 103c) much shorter and more swollen than in the other two species. There are clear terminal genitalia differences between the three dissected species. Two of these, *H. fusca* and *H. rotula*, show rather marked departures from the typical pattern seen in species of *Semperdoninae*. As such, I interpret them as indications of character divergence to reinforce species separation.

Since only Kondo, in 1949, attempted fieldwork on Guam that was keyed toward collecting at local stations, there are fruitful opportunities for comparative investigations of the *Himeroconcha* species.

Within the genus, there are two divergent conchological specializations. *Himeroconcha lamlanensis* (fig. 104d–f) has a depressed spire, looser coiling pattern, reduced whorl count, thinner shell, and reduced sculpture. *Himeroconcha rotula* (fig. 104a–c), *H. quadrasi* (fig. 105a–c), and *H. fusca* (fig. 105d–f) show progressive radial rib reduction and size increment that is partly caused by increased peripheral angulation (*H. quadrasi*) and partly (*H. fusca*) by actual enlargement of the shell. The 6.1% increase in mean diameter and 7.6% decrease in H/D ratio between *H. rotula* and the slightly larger *H. quadrasi* can be attributed to the change from a rounded to obtusely angulated periphery in the latter species. The much greater size difference between *H. quadrasi* and *H. fusca*, a 26.4% increase in mean diameter with less than one-quarter additional whorl added and only a change from an obtusely to acutely angulated periphery, is much too large to be interpreted as resulting from simple form alterations. Instead, actual size change of the organism is involved.

*Ladronellum* is most apt to be confused with *Himeroconcha*. In color, size, and general sculptural appearance, *Ladronellum mariannarum* (fig. 101a–c) compares quite well with *Himeroconcha rotula* (fig. 104a–c). There are both conchological and anatomical differences. *Ladronellum* has apertural barriers, lacks the very prominent secondary spiral cording on the

shell, and has a much more elevated spire and a greater number of more tightly coiled whorls at similar diameters. In the genitalia, *Ladronellum* has a very long and slender vagina (fig. 102a), and the penis (fig. 102d) has a totally changed pilaster system. A huge, inflatable horseshoe-shaped pilaster occupies the lower two-thirds to half of the penis and frequently extends into the atrium. Pallial structures in *Ladronellum* and *Himeroconcha* are essentially identical. *Semperdon* (figs. 97–99) differs most obviously in its flammulated or reddish color pattern, total absence of any secondary spiral sculpture, much finer and more numerous radial ribs, and normally many apertural barriers. Its pallial cavity has the rectal kidney lobe twice the length of the pericardial (fig. 100a), but the latter is not narrowed. The major genital change concerns insertion of the vas deferens on the epiphallic head right next to the penial retractor insertion (fig. 100k) rather than below the penis head as in *Himeroconcha* (fig. 103a).

The name *Himeroconcha* refers to the unusual and beautiful shell color and sculpture of the species.

***Himeroconcha lamlanensis*, new species.** Figures 103a–b, 104d–f.

**Diagnosis.**—Shell large, diameter 3.94–3.97 mm. (mean 3.96 mm.), with  $3\frac{1}{2}$ –3% rather loosely coiled whorls. Apex and spire sunken beneath level of body whorl, last part of body whorl descending moderately, H/D ratio 0.450–0.487 (mean 0.469). Apical sculpture of 7–8 (mean 7.5) fine spiral cords, whose interstices are about 4–5 times their width. Postnuclear sculpture of low, irregular, protractively sinuated radial ribs, about 31–35 on the body whorl, which have periostracal extensions and whose interstices are highly variable. Frequently ribs not distinguishable from growth wrinkles. Microsculpture reduced, occasionally clear indication of fine radial riblets and finer spiral riblets visible, but no clear indication of whether secondary sculpture is grooves or cording because of growth irregularities. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 3.31–3.54 times (mean 3.43) in the diameter, margins strongly rounded. Sutures impressed, whorls strongly rounded above, flattened laterally above periphery and on basal margin, with evenly rounded periphery. Aperture subcircular, flattened laterally above periphery and on basal margin, inclined about 20° from shell axis, without barriers.

*Himeroconcha lamlanensis* (fig. 104d–f) differs from the other Mariana Island species in its depressed apex and spire. The Ponape Island *Russatus nigrescens* (fig. 89e–f) is very similar in form and general appearance, but differs in its narrow umbilicus, much more crowded and irregular sculpture, looser coiling pattern, and darker color.

**Description.**—Shell large, with  $3\frac{1}{2}$  loosely coiled whorls. Apex and early spire depressed below plane of penultimate whorl, last whorl moderately descending, H/D ratio 0.450. Embryonic whorls 1%, sculpture of 7 low, widely spaced spiral ribs, with vague indication of widely spaced, protractive radial riblets on last quarter whorl. Remaining whorls with lamellar, somewhat irregularly spaced, protractively sinuated radial ribs, 35 on the body whorl, whose interstices are usually 4–6 times their width. Microsculpture of occasional fine radial riblets and finer spiral riblets. Sutures deep, whorls strongly rounded above and on periphery, flattened laterally both above and below. Umbilicus broadly open, cup-shaped, regularly decoiling, contained 3.54 times in the diameter. Color of apical whorls light yellow-horn, lower whorls progressively darker with termination of body whorl a deep reddish purple. Aperture ovate, equally flattened above and below periphery, inclined about 20° from the shell axis. Height of holotype 1.78 mm., diameter 3.94 mm.

**Holotype.**—Mariana Islands: Guam, Station 137, near summit of Mt. Lamlan at 1,300 ft. elevation. Collected by Yoshio Kondo on October 28, 1949. BPBM 215025.

**Range.**—Summit of Mt. Lamlan, Guam, Mariana Islands.

**Paratype.**—Guam: Mt. Lamlan (Station 66) at 1,334 ft. elevation (1 specimen, BPBM 213435).

**Remarks.**—Although *Himeroconcha rotula* has an elevated spire, is more than half a millimeter larger in mean diameter, and averages three-quarters of a whorl more (table LIII), *H. lamlanensis* can be derived from that species by a few simple modifications. Depression of the apex and spire, shifting of the whorl flattening from the lower palatal wall to the basal margin, reduction in sculpture, loosening in coiling pattern, and reduction in whorl count are the required changes. Some of the above changes tend to be correlated. Despite an initial quite different appearance, I have no hesitation in considering them to belong to the same genus. Anatomical differences between the species of *Himeroconcha* are covered in the generic discussion above.

*Russatus nigrescens* (fig. 89e–f) from Ponape, Caroline Islands, shows many differences from *H. lamlanensis* despite superficially similar appearance. The similarities all result from the reduced whorl count and sculpture. Any comparison of anatomical structure shows that they are totally unrelated and cannot be confused.

Despite intensive efforts by Dr. Kondo, only two specimens were obtained on Mt. Lamlan, compared with 20 *H. fusca*, 127 *Ladronellum mariannarum*, and nine *Semperdon heptapychius* from the same two stations.

**Description of soft parts.**—Terminal genitalia and pallial cavity of 1 broken individual studied.

Pallial cavity with upper end torn, part of kidney missing. Ureter with arms tightly compressed, no lung roof showing even at tip, opening anteriorly just beside anus. Kidney with rectal and pericardial lobes equal in length, total length of kidney probably about 2.1 mm. Part of rectal lobe near middle extending very slightly onto parietal wall, kidney sharply tapering apically to a thin sheet of tissue. Heart and pulmonary vein typical.

Prostate (fig. 103a, DG) and uterus (UT) very short, structurally as in *H. fusca*. Vas deferens (VD) very thin-walled to penioviducal angle, diameter equal to free oviduct, after reflexion very narrow and with muscular walls, inserting into side of epiphallus distinctly below attachment of penial retractor. Epiphallus (E) equal in diameter to lower part of vagina, a coiled double cylinder with inner invaginated. Penial retractor (PR) shorter than epiphallus, arising from diaphragm, inserting on head of latter. Epiphallus entering upward extended collar of muscle sheath and narrowing abruptly before opening into penial chamber (fig. 103b) through a simple pore. Penis (P) about 2.0 mm. long, with a heavy muscular collar extended upward around base of epiphallus. Walls of penis chamber separable from muscle sheath only with great difficulty. Interior of penis with many very narrow and high pilasters radiating from vas deferens pore to midsection, where they fuse into three large pilasters that taper to atrium (Y).

Free oviduct (UV) very short, internally with narrow pilasters. Spermatheca (S) with elongated and expanded head, shaft very slender until level of free oviduct, then rapidly expanding with internal pilaster type structures. Vagina (V) gradually tapering from sper-



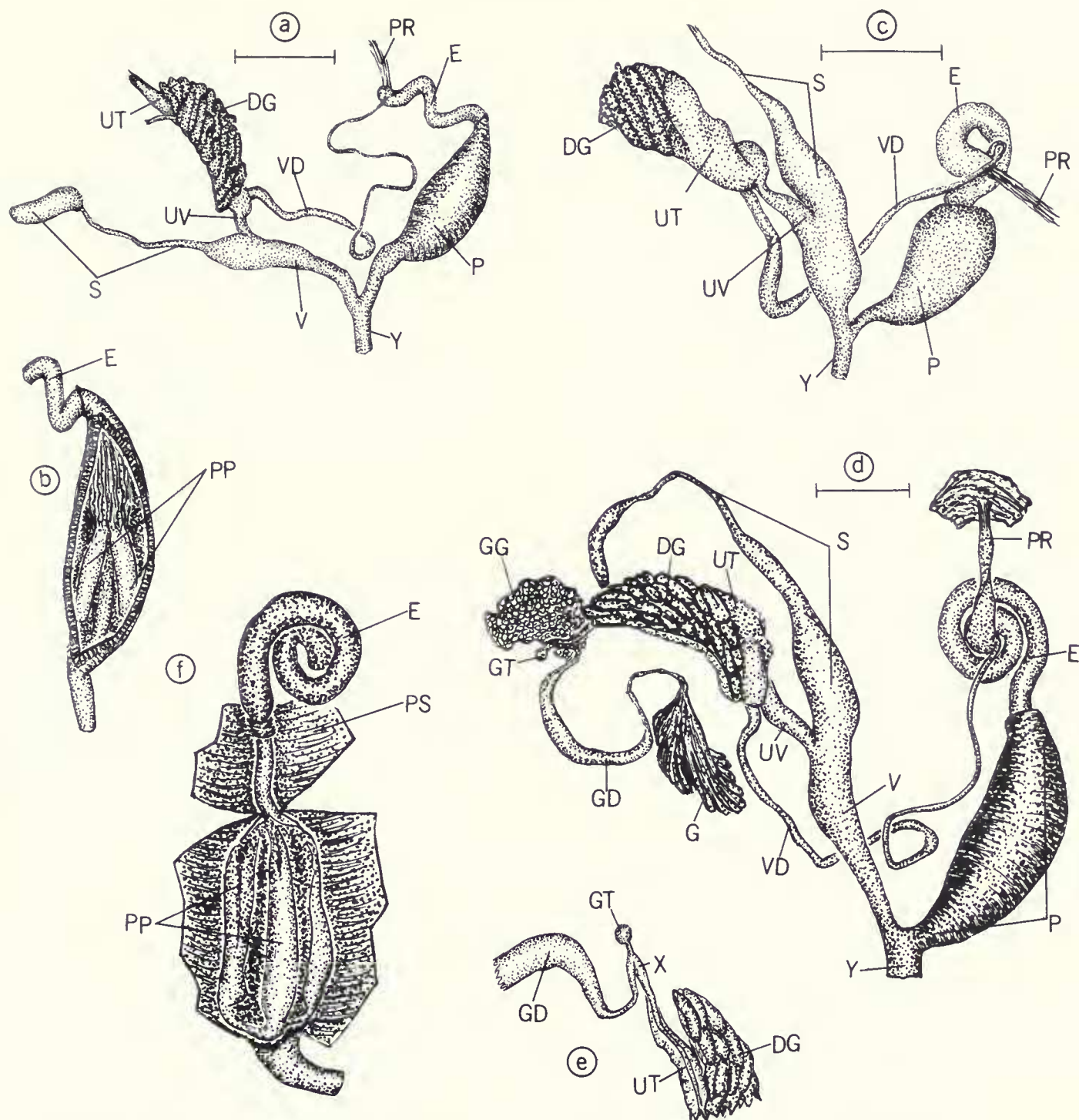


FIG. 103. Anatomy of *Himeronconcha*: a–b, *Himeronconcha lamlanensis*. Station 137, Mt. Lamlan, Guam. BPBM 215025. a, genitalia. b, interior of penis; c, genitalia of *Himeronconcha rotula* (Quadras & Möllendorff). Ukudu, Guam. BPBM 82741; d–f, *Himeronconcha fusca* (Quadras & Möllendorff). Station 137, Mt. Lamlan, Guam. BPBM 215020. d, genitalia. e, detail of midvisceral genitalia; f, interior of penis. Scale lines equal 1 mm. (MO).

mathecal opening to atrium with internal pilasters decreasing in size. Atrium (Y) rather long.

Jaw not successfully mounted.

Radula with 6 laterals and more than 6 marginals. Central tooth smaller than 1st lateral, width about  $8\ \mu$ , length about  $13\ \mu$ . First lateral about  $11\ \mu$  wide,  $14\text{--}15\ \mu$  long.

(Based on BPBM 215025, 1 fragmentary example.)

***Himeronconcha rotula*** (Quadras & Möllendorff, 1894). Figures 103c, 104a–c.

*Patula rotula* Quadras & Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), pp. 13–14—Mariana Islands.

*Patula rotula* (form) *pallens* Quadras & Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), p. 14.

*Patula rotula* var(iety) *intercedens* Quadras & Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), p. 14.

*Endodonta* (*Charopa*) *rotula* (Quadras & Möllendorff), Pilsbry, 1895, Man. Conchol., (2) 9, p. 340.

**Diagnosis.**—Shell large, diameter 4.05–5.53 mm. (mean 4.57 mm.), with 4–4½ normally coiled whorls. Apex and spire slightly to moderately and evenly elevated, body whorl descending much more

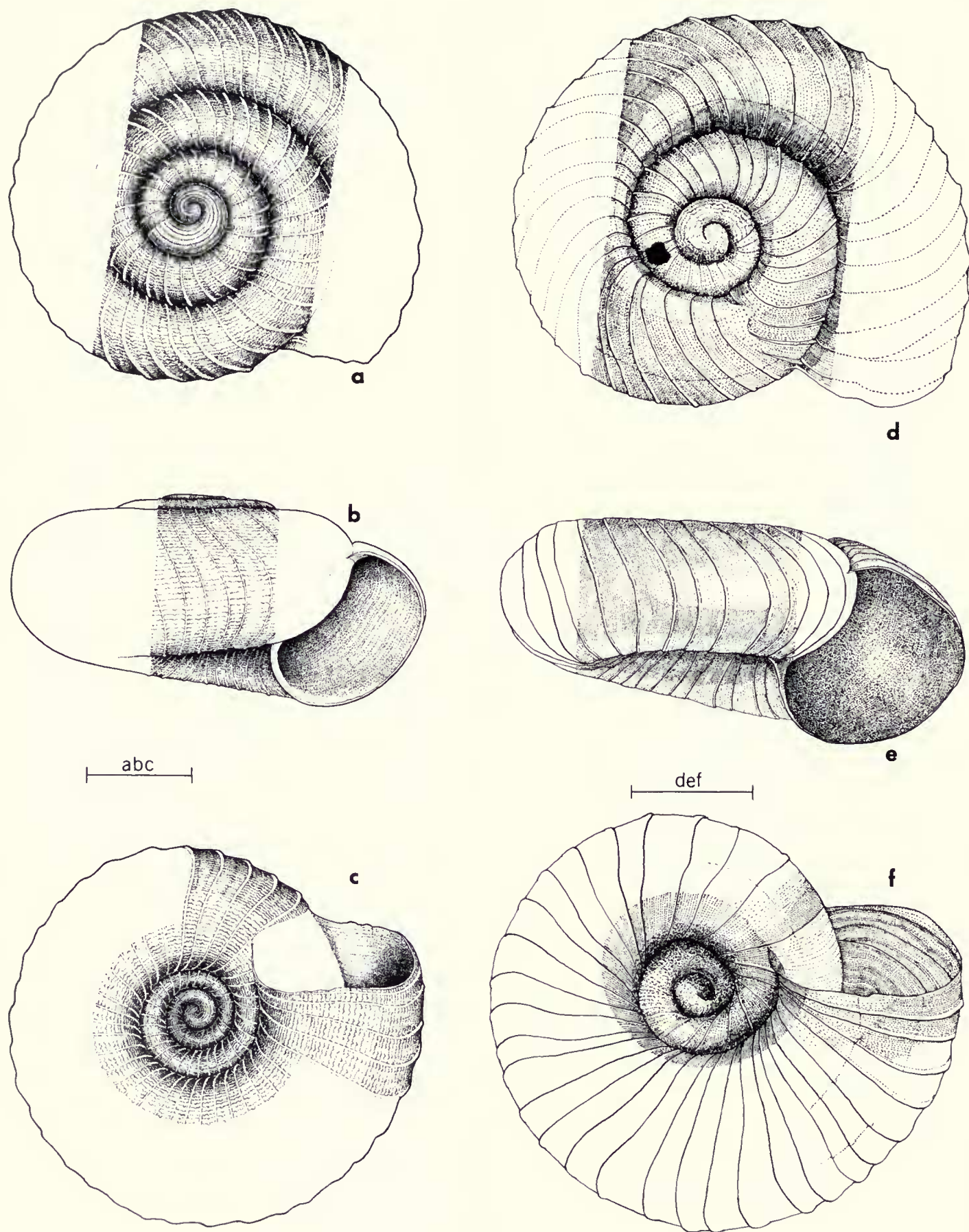


FIG. 104. a-c, *Himeroconcha rotula* (Quadras & Möllendorff). Guam. Paratype. BPBM 87457 ex SMF; d-f, *Himeroconcha lamlanensis*, new species. Station 137, Mt. Lamlan, Guam, Mariana Islands. Holotype. BPBM 215025. Scale lines equal 1 mm. (a-c, MM; d-f, SH).



rapidly, spire protrusion  $\frac{1}{6}$ – $\frac{1}{7}$  body whorl width, H/D ratio 0.440–0.554 (mean 0.497). Apical sculpture of 7–11 (mean 8.7) very prominent spiral cords, whose interstices are about twice their width, with accessory spiral cords in upper suture. Postnuclear sculpture of low and irregular, protractively sinuated, widely spaced radial ribs, 34–42 on the body whorl, whose interstices are highly variable. Microsculpture of fine radial riblets and much finer spiral riblets that are completely dominated by prominent, rather crowded secondary spiral cords, whose interstices are about twice their width and which are several times as large as the microradials. Umbilicus broadly V-shaped, regularly decoiling, contained 3.17–4.06 times (mean 3.51) in the diameter, margins strongly rounded. Sutures deep, whorls strongly rounded above, flattened laterally above, and compressed laterally below rounded periphery. Aperture subcircular, strongly flattened laterally above periphery, inclined about 30° from shell axis, without barriers.

*Himeroconcha rotula* (fig. 104a–c) differs from *H. quadrasi* and *H. fusca* (fig 105a–f) in its rounded periphery and smaller size, from *H. lamlanensis* (fig. 104d–f) by its elevated (not sunken) spire and prominent secondary spiral cording. *Ladronellum marianarum* (fig. 101a–c) is a much smaller, higher shell with apertural barriers.

*Description.*—(*rotula*)—Shell large, with  $4\frac{1}{4}$  normally coiled whorls. Apex and early spire flat, body whorl descending moderately, H/D ratio 0.440. Apical whorls slightly more than  $1\frac{1}{2}$ , sculpture of 8 major spiral ribs, crossed by relatively fine radial ribs with faint traces of microspiral reticulation. Remaining whorls with irregular, moderately prominent, widely spaced, protractively sinuated radial ribs, crossed by wavy, prominent secondary spiral cords with faint traces of microreticulation occasionally visible. Sutures deep, whorls strongly rounded at shoulder, somewhat flattened laterally above bluntly rounded periphery, with evenly rounded basal and columellar margin. Periphery not protruding or carinated. Umbilicus broadly V-shaped, last whorl decoiling more rapidly, contained 3.57 times in the diameter, with slightly reflexed lip edge and rounded margins. Height of lectotype 2.16 mm., diameter 4.90 mm.

(*pallens*)—Shell large, with  $4\frac{1}{4}$  normally coiled whorls. Apex flat, upper whorls of spire barely descending, last whorl dropping more sharply, H/D ratio 0.481. Apical whorls  $1\frac{1}{2}$ , sculpture of 9 major spiral ribs crossed by fine radial riblets with faint traces of spiral reticulation. Remaining whorls with broadly rounded, irregularly spaced, protractively sinuated radial ribs crossed by prominent wavy spiral ribs with faint microreticulation visible. Sutures deep, whorls strongly rounded above, slightly flattened laterally above the bluntly angulated periphery, with evenly rounded baso-columellar margins. Umbilicus broadly V-shaped, regularly decoiling, contained 3.44 times in the diameter, with rounded margins. Color very light reddish yellow-brown. Aperture subcircular, slightly flattened laterally above periphery, inclined about 15° from the shell axis. Height of lectotype 2.48 mm., diameter 5.17 mm.

(*intercedens*)—Shell large, with  $4\frac{1}{2}$  normally coiled whorls. Apex flat, whorls of spire descending progressively more rapidly, H/D ratio 0.488. Apical whorls  $1\frac{1}{2}$ , sculpture of 7 major spiral ribs, crossed by a microsculpture of moderately prominent radial riblets with traces of spiral reticulations. Remaining whorls with irregularly spaced, relatively prominent, protractively sinuated radial ribs, crossed by relatively regularly spaced, wavy, moderately prominent spiral riblets with faint microsculpture of radial and spiral riblets occasionally visible. Sutures deep, whorls strongly rounded above, slightly flattened laterally above periphery with evenly rounded basal margin and strongly rounded columellar margin. Umbilicus V-shaped, regularly decoiling, contained 3.50 times in the diameter with strongly rounded margins. Color dark reddish yellow-brown, apex much lighter in tone. Periphery of body whorl bluntly rounded without definite keel or rostration. Aperture subcircular, strongly flattened laterally above periphery with slightly flattened baso-palatal margin, inclined about 25° from shell axis. Baso-columellar lip with moderately prominent callus. Height of lectotype 2.68 mm., diameter 5.49 mm.

*Lectotypes.*—Mariana Islands: Guam. Collected by Quadras. SMF 165348 (*rotula*); SMF 165350 (*pallens*); SMF 165344 (*intercedens*).

*Range.*—Guam, Mariana Islands.

*Paratypes.*—SMF 165349, SMF 165351, SMF 165345, BPBM 86192–4, BPBM 87457–8.

*Material.*—Guam (10 specimens, SMF 165344, SMF 165349, SMF 165350, FMNH 46311): Ukudu, 2 miles inland in Dededo municipality at 300 ft. elevation (1 specimen, BPBM 82741, collected on November 10, 1925, by H. G. Hornbostel).

*Remarks.*—Only one specimen has been taken since description of the types. None of the other *Himeroconcha* have been found near Ukudu so that the geographic relationships of these species are unknown. Dissection of the one *H. rotula* showed that the penis was short, 1.6 mm. long, lacked the small pilasters in the upper part of the penis, and had the three major pilasters narrower than those found in *H. fusca*. Probably these differences are enough to ensure species isolation.

Quadras & Möllendorff (1894) proposed two varietal names, *pallens* for a light-colored shell and *intercedens* for a flatter, more widely umbilicated shell with obtuse angulation to the periphery. These are extreme individual variations and are not representative of populations. The apparent peripheral angulation claimed for *intercedens* is a visual artifact accompanying the lower spire and hence flatter upper palatal spire contour. There is no actual angulation to the periphery.

*Himeroconcha rotula* is only slightly smaller than *H. quadrasi*, but differs most obviously by the strongly angulated periphery and lower H/D ratio of the latter. *Himeroconcha fusca* is very much larger and prominently keeled; *H. lamlanensis* is smaller, has a depressed apex and spire, and lacks the very prominent secondary spiral cording.

*Description of soft parts.*—Fragmentary genitalia from one adult were available. Apical genitalia and pallial organs missing. Terminal genitalia (fig. 103c) agreeing with *H. fusca* except in having vagina (V) proportionately much thicker and narrowing abruptly to atrium and penis (P) shorter and thicker. Penis 1.6 mm. long, ovate, internal apical portion smooth, lower 3 pilasters much narrower than in *H. fusca*.

Jaw not mounted successfully.

Radula with 2 laterals and more than 7 marginals. Central tooth typical, about 8  $\mu$  wide and basal plate 11  $\mu$  long. First lateral about 11  $\mu$  wide and 12  $\mu$  long.

(Based on BPBM 82741.)

### *Himeroconcha quadrasi* (Möllendorff, 1894). Figure 105a–c.

*Patula quadrasi* Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), p. 14—Mariana Islands.

*Endodonta (Charopa) quadrasi* (Möllendorff), Pilsbry, 1895, Man. Conchol., (2) 9, p. 340; Gude, 1896, Science Gossip, 3 (27), p. 58, fig. 5—Guam, Mariana Islands.

*Diagnosis.*—Shell very large, diameter 4.54–5.13 mm. (mean 4.85 mm.), with  $4\frac{1}{4}$ – $4\frac{1}{2}$  normally coiled whorls. Apex and spire moderately and usually evenly elevated, body whorl descending slightly



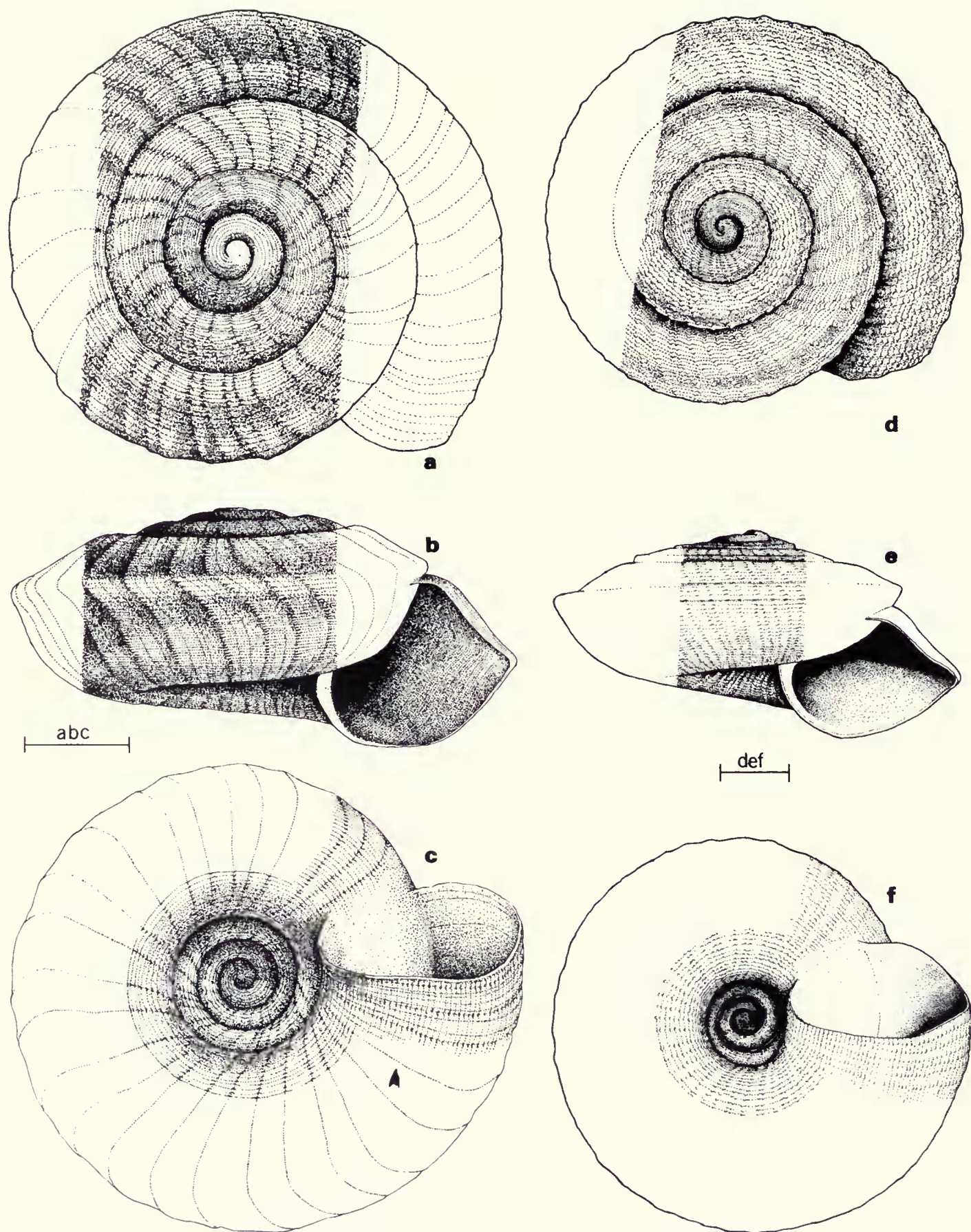


FIG. 105. a–c, *Himeroconcha quadraasi* (Möllerndorff). Guam, Mariana Islands. Paratype. BPBM 87455; d–f, *Himeroconcha fusca* (Quadras & Möllerndorff). Guam, Mariana Islands. Paratype. BPBM 87456. Scale lines equal 1 mm. (MM).



more rapidly, spire protrusion more than  $\frac{1}{4}$  body whorl width, H/D ratio 0.419–0.496 (mean 0.461). Apical sculpture of 8–12 (mean 9.7) prominent spiral cords, whose interstices are about twice their width, with secondary spiral and radial elements visible between major cords. Postnuclear whorls with irregular remnants of strongly protractively sinuated radial ribs intermingled with growth wrinkles. Microsculpture of fine radial riblets and finer spiral riblets with much more prominent, rather crowded secondary spiral cording, whose interstices are less than 3 times their width. Umbilicus broadly V- to U-shaped, regularly decoiling, contained 3.12–4.56 times (mean 3.70) in the diameter, margins rounded. Sutures shallow, whorls flatly rounded down to obtusely angulated and slightly protruded periphery, with evenly rounded basal margin after lateral flattening below periphery. Aperture subrectangular, periphery slightly protruded, inclined about 20° from shell axis.

*Himeroconcha quadrasi* (fig. 105a–c) is immediately separated from *H. rotula* (fig. 104a–c) by its angulated and protruded periphery. *Himeroconcha fusca* (fig. 105d–f) averages more than 1 mm. larger, has a proportionately narrower umbilicus, and the apical cording is reduced in prominence.

**Description.**—Shell very large, with slightly more than 4% normally coiled whorls. Apex and early spire slightly and evenly elevated, lower whorls descending a little more rapidly, H/D ratio 0.447. Apical whorls 1%, sculpture of 8 prominent major spiral ribs crossed by a microsculpture of very fine, crowded radial riblets with slight traces of very faint spiral reticulations, first fraction of a whorl almost smooth, only granulosely pitted. Remaining whorls with irregularly spaced, broadly rounded, somewhat prominent radial ribs crossed by wavy, moderately crowded, and prominent secondary spiral cords. Faint microsculpture of very fine radial and spiral riblets, visible on portions of shell. Sutures shallow, whorls flatly rounded above with slight supraperipheral sulcation. Periphery with bluntly rounded, slightly protruding carina, not obviously rostrate. Umbilicus V-shaped, regularly decoiling, contained 3.62 times in the diameter, with rounded margins, edge of columellar lip slightly reflected. Color reddish yellow-horn without darker flammulations, apex light yellow-brown. Aperture ovate, flatly rounded above bluntly protruding periphery, almost evenly rounded on basal and columellar margins, inclined about 20° from shell axis. Height of lectotype 2.22 mm., diameter 4.97 mm.

**Lectotype.**—Marianas: Guam. Collected by Quadras. SMF 165346.

**Range.**—Guam, Mariana Islands.

**Paratypes.**—BPBM 86195, BPBM 87455, SMF 165347.

**Material.**—Guam (7 specimens, BPBM 167438, FMNH 18885, FMNH 46251, FMNH 46312–3).

**Remarks.**—A considerable number of additional specimens are scattered through museum collections bearing the locality "Marianas" or "Mariana Islands." These were not measured or utilized in this study. No specimens with exact locality data were seen. The relationship of *Himeroconcha quadrasi* to *H. fusca* will remain uncertain until the former can be dissected. *Himeroconcha fusca* is a greatly enlarged, more narrowly umbilicated version of *H. quadrasi*. Without exact localities and preserved material for the latter, whether they are geographic replacements or sympatric taxa cannot be determined.

Size, shape, and sculptural differences are sufficiently large that I have no hesitation in calling *H. quadrasi* and *H. fusca* distinct species.

## ***Himeroconcha fusca* (Quadras & Möllendorff, 1894). Figures 103d–f, 105d–f.**

*Patula fusca* Quadras & Möllendorff, 1894, Nachr. d. Malak. Gesell., 26 (1–2), p. 13—Mariana Islands.

*Endodonta (Charopa) fusca* (Quadras & Möllendorff), Pilsbry, 1895, Man. Conchol., (2) 9, p. 340; Gude, 1896, Science Gossip, 3 (27), pp. 58–59, fig. 6—Guam, Mariana Islands.

**Diagnosis.**—Shell extremely large, diameter 5.59–7.04 mm. (mean 6.13 mm.), with  $4\frac{1}{4}$ – $4\frac{3}{4}$  normally coiled whorls. Apex and spire usually moderately and evenly elevated, rarely flat or slightly elevated, body whorl descending more rapidly and deflected below periphery of penultimate, spire protrusion normally slightly less than  $\frac{1}{4}$  body whorl width, H/D ratio 0.388–0.550 (mean 0.464). Apical sculpture of 8–12 (mean 10.2) wavy, rather crowded spiral cords crossing lower, protractive, irregular, and more crowded radial ribs. Postnuclear sculpture of vague major radial ribs and irregular growth wrinkles crossed by narrow, very crowded prominent secondary spiral cords. Typical microreticulation, with spirals much finer, occasionally visible under high magnification. Umbilicus narrowly U-shaped, regularly decoiling, contained 4.00–5.81 times (mean 4.44) in the diameter, margins rounded. Sutures very shallow, whorls flatly rounded down to distinct supraperipheral sulcus, periphery protruded and acutely angulated, with weak subperipheral sulcus and evenly rounded lower margins. Aperture subquadrangular, strongly flattened above protruded periphery, inclined about 30° from shell axis.

*Himeroconcha fusca* is by far the largest Micronesian charopid land snail. It differs from *H. quadrasi* (fig. 105a–c) in its narrower umbilicus, acutely angulated periphery, stronger radial elements in the apical sculpture, and much larger size. *Himeroconcha rotula* (fig. 104a–c) is very much smaller and lacks the peripheral angulation seen in the two species mentioned above.

**Description.**—Shell extremely large, with slightly less than 4% normally coiled whorls. Apex and early spire nearly flat, later whorls descending more rapidly, body whorl slightly depressed beneath periphery of penultimate, H/D ratio 0.453. Embryonic whorls 1%, irregular sculpture of moderately prominent spiral ribs crossed by narrow to wide and crowded radial ribs. Remaining whorls with irregularly prominent growth wrinkles crossed by a marked microsculpture of wavy spiral cording with fine traces of microradial ribs barely visible. Sutures shallow, whorls moderately flat above with slight supraperipheral concavity. Periphery carinate, moderately protruding, slightly denticulated by crossings of major growth wrinkles. Umbilicus narrowly U-shaped, barely decoiling, contained 4.31 times in the diameter, with rounded margins and edge of lip slightly reflected. Color light yellow-reddish brown without darker flammulations, apex yellow-horn. Aperture ovate, strongly flattened above rostrate peripheral margin, evenly rounded basally with strongly rounded columellar margin inclined about 25° from the shell axis. Height of lectotype 2.81 mm., diameter 6.21 mm.

**Lectotype.**—Marianas: Guam. Collected by Quadras. SMF 165342.

**Range.**—Guam, Mariana Islands.

**Paratypes.**—BPBM 86191, BPBM 87456, SMF 165343.

**Material.**—Guam (9 specimens, FMNH 18886–7, FMNH 46340, FMNH 46345, BPBM 167437); Talofofo (Station 134), between cave and road (2 specimens, BPBM 215250); Mt. Lamalan (Station 137) at 1,300 ft. elevation (23 specimens, BPBM 215020–4).

**Remarks.**—In having a strong intrusion of radial elements into the apical sculpture, *Himeroconcha fusca*

is the most modified charopid species in the Mariana Islands. The acute peripheral angulation, great size, and degree of major rib reduction also mark it as being highly modified. Dissection showed that the penis is very long, 2.6–2.8 mm., and that the formation of three fused pilasters occurs proportionately higher in the penis (fig. 103f) than in the other *Himeroconcha* dissected. Otherwise the anatomy shows no unusual features.

Live specimens were obtained at Station 137 on Mt. Lamalan together with *Ladronellum mariannarum*, *Semperdon heptptychius*, and *Himeroconcha lamalanensis*, but none were taken at nearby Station 66. Probably colonies of *H. fusca* are severely limited in extent.

*Description of soft parts.*—Foot and tail equal to or slightly shorter than shell diameter, very slightly tapering posteriorly. Sole and pedal grooves typical, latter meeting above tail without marked depression, no caudal horn or middorsal groove developed. Slime network indistinct. Head projecting slightly in front of foot. Ommatophores very long. Gonopore below right ommatophore and behind right rhinophore.

Body color light yellow-white on foot and tail, back of head and ommatophores light reddish gray, edge of mantle collar yellow-white.

Mantle collar thick, edges curled in preservative, no glandular extension onto pallial roof. Pneumostome can be closed by a mantle lobe. Anus opening very slightly in front of external ureteric pore, both just inside pneumostome with a distinct channel leading to exterior.

Pallial region extending  $\frac{2}{3}$  whorl apically. Lung roof clear, without granulations. Kidney bilobed, about 2.8 mm. long, apical margin rounded, rectal lobe scarcely longer than pericardial, posterior mid-portion extending across hindgut and slightly onto parietal wall. Pericardial lobe of kidney narrower than rectal. Ureter with arms tightly compacted between kidney lobes, sometimes anterior tip with lung roof visible between. Heart more than half length of pericardial kidney lobe, angled slightly from hindgut. Principal pulmonary vein very faint, unbranched. Hindgut deflected from parietal-palatal margin just at rounded end of kidney.

Ovotestis (fig. 103d, G) a single clump of palmately clavate alveoli, located above stomach apex, individual alveoli rather numerous. Hermaphroditic duct (GD) not convoluted, without unusual features. Albumen gland (GG) short and compact, acini small. Talon (fig. 103e, GT) and carrefour (X) agreeing in structure with *Ladronellum mariannarum*. Prostate (DG) of a few large acini opening into groove on inner wall of uterine chamber. Uterus (UT) bipartite, lower chamber with thick glandular walls complexly folded.

Vas deferens (VD) fairly large in diameter at first, walls thin and 2 longitudinal pilasters visible down to level of penioviducal angle, becoming very slender and muscular on apical reflexion. Epiphallus (E) long, tightly coiled, sometimes around penial retractor muscle, vas deferens entering a little below head of epiphallus. Internally, epiphallus with folded tube. Below penis sheath collar epiphallus much narrower. Penial retractor (PR) arising from diaphragm, shorter than epiphallus, inserting on head of epiphallus distinctly above lateral insertion of vas deferens. Penis (P) long and slender, with a heavy muscle sheath extending upward as a collar around base of epiphallus. Length from sheath apex to atrium about 2.6–2.8 mm. Internally (fig. 103f), penis with epiphallus opening through a simple pore, upper part of penis with very numerous longitudinal pilasters that soon coalesce into 3 large pilasters (PP). These fuse at penis base. Walls of penis very muscular. Atrium (Y) of average length.

Free oviduct (UV) short, about 1.0 mm. long, thin-walled, with longitudinal pilasters, narrower in diameter than vagina. Sper-

matheca (S) with very slender and elongated head lying above albumen gland, shaft slender at first, gradually enlarging to level of free oviduct, then grossly expanded. Vagina (V) thick at first, gradually tapering to atrium. Spermathecal base and vagina internally with longitudinal pilasters and a complex huge pilaster at base of spermathecal shaft.

Muscle and digestive systems without unusual features.

(Based on BPBM 215020, several whole and fragmentary specimens.)

#### INCERTAE SEDIS

Every systematic review of a major group inevitably concludes with a list of names that cannot be associated with known populations. Whether they are the result of erroneous locality data, careless systematic work, lost type specimens, or represent species not collected subsequently often cannot be determined. Five such names are discussed below in chronological order. Of these, *Helix oceanica* cannot be identified, *Helix rotula* probably was badly illustrated and described, *Helix multispinata* probably was cited erroneously from the Pacific Islands, whereas *Helix minutialis* and *Pithys verecunda* possibly are valid species that have not been collected subsequently and whose types are lost.

The type of a sixth species, *Helix filiola* Férussac (1840, pl. 86, fig. 1) was recently located in the collection of the Museum National d'Histoire Naturelle by Dr. Simon Tillier. Through his kind cooperation, it was possible to inspect this unique specimen in October 1981. Although Pilsbry (1893–1895, p. 35) had tentatively listed this species as a *Charopa*, it is a rhytidid. The same species was described shortly thereafter as *Helix gradata* Gould, 1848, and has subsequently been referred to in the literature usually as *Ouagapia gradata* (Gould, 1848). A probably more correct generic allocation would be to *Torresiropa* Iredale (1933) (see Solem, 1959b). To my knowledge, Férussac's name has not been mentioned in literature since 1893. The question as to whether his name should replace Gould's appellation is left to rhytidologists.

#### *Helix oceanica* Le Guillou, 1842.

*Helix oceanica* Le Guillou, 1842, Rev. et Mag. Zool., 5, p. 140—Tahiti; Pfeiffer, 1848, Monog. helic. viv., 1, p. 120; Pfeiffer, 1876, Monog. helic. viv., 7, p. 203; Ponsonby, 1910, Proc. Malacol. Soc. London, 9 (1), p. 37.

*Pithys oceanica* (Le Guillou), Pease, 1871, Proc. Zool. Soc. London, 1871, p. 475.

*Remarks.*—A specimen in the Museum National d'Histoire Naturelle, Paris, from the Le Guillou collection is labeled as this species. The apex is broken and missing, while the shell sculpture is almost completely eroded. In size and shape the shell is extremely close to both *Libera dubiosa* Ancey and *Libera garrettiana* Solem. The specimen is so worn and damaged that it is impossible to say which species it represents. Since the only potential type specimen is unidentifiable and the name has been dormant for so long, R.I.P.



***Helix minutialis* Deshayes, 1851.**

*Helix minutialis* "Ferussac" Deshayes, 1851, Hist. Nat. Moll. terr. fluv., 1, p. 83—sur les hautes montagnes, Taiti (=Tahiti, Society Islands); Pfeiffer, 1853b, Monog. helic. viv., 3, p. 91; Pfeiffer, 1859, Monog. helic. viv., 4, p. 84; Pfeiffer, 1876, Monog. helic. viv., 7 p. 148.

*Helicopsis minutialis* (Férussac), Pease, 1871, Proc. Zool. Soc. London, 1871, p. 475.

**Remarks.**—Although plate references accompanied the original description, that particular plate, 82A, apparently never was issued. The meager description and more copious notes accompanying the description effectively exclude any known adult Tahitian shell or the young of *Libera*. They strongly suggest *Discocharopa*, or, less probably, *Striatura*, neither of which are known from Tahiti. Possibly this is a species of *Punctum*, one specimen of which is known from Tahiti (p. 57). No specimens could be located, and this name cannot be identified.

For convenience, the original description and notes are copied below:

H. Testa minima, orbiculato-depressa, alba, hyalina, substriata, late umbilicata; anfractibus convexiusculis, angustis; apertura rotundato-semilunari, obliqua, simplici; marginibus acutissimis.

Habite l'île de Taiti, sur les hautes montagnes (Cuming).

**DESCRIPTION.** Jolie petite espèce qui a beaucoup de rapports avec l'*helix pygmaea* qui vit en France. Elle est orbiculaire, très aplatie à spire peu saillante au-dessus du dernier tour. Cette spire est un peu convexe, très obtuse au sommet, et l'on y compte quatre tours et demi peu convexes, à suture simple et superficielle. Le dernier tour est cylindracé, convexe à la circonférence, et un peu plus large en dessous qu'en dessus. Les tours s'élargissent lentement, et le dernier, sous ce rapport, est proportionné avec les précédents. Un large ombilic, dont le diamètre est un peu plus grand que celui du dernier tour, occupe toute la base de la coquille. L'ouverture est arrondie, sem-lunaire; elle est simple, et ses bords sont minces et tranchants. L'espace qui sépare les deux extrémités du bord égale un peu plus de la moitié de la circonférence de l'avant-dernier tour. Il faut observer cette très petite coquille sous un grossissement assez fort pour apercevoir les stries nombreuses, peu profondes et très serrées dont elle est couverte. A l'oeil nu, la coquille est lisse et brillante. Elle est très mince, très fragile, et d'un blanc jaunâtre ou verdâtre uniforme.

Cette petite espèce a 2 millimètres de diamètre, et à pleine 1 millimètre d'épaisseur.

***Helix multispirata* Hombron & Jacquinot, 1852.**

*Helix multispirata* Hombron & Jacquinot, 1852, Voy. Pol. Sud, Astrolabe et Zélée, Atlas of Shells, pl. 11, figs. 9–12—Vavau, Tonga; Rousseau, 1854, Voy. Pol. Sud, Astrolabe et Zélée, 5, p. 53; Pfeiffer, 1859, Monog. helic. viv., 4, p. 178; Pfeiffer, 1876, Monog. helic. viv., 7, p. 282; Tryon, 1887, Man. Conchol., (2) 3, p. 127, pl. 26, figs. 16–18; Pilsbry, 1894, Man. Conchol., (2) 9, p. 84—States as probably a "Charopa."

**Remarks.**—No specimens of this problematic species could be located. The illustrations suggest that possibly this is a near relative of the Samoan *Sinployea allecta allecta* (Cox) (fig. 54a–c) and Swains Island *Sinployea intermedia* (fig. 52d–f). It is not the Vavau Island *Sinployea vicaria* (Mousson) (fig. 58a–c), because that species has an elevated spire, whereas the illustrations of *Helix multispirata* show a flat-spined

shell. Collections made on Vavau by Laurie Price in late 1965 produced nothing that resembled the illustrations. I suspect that the locality cited is in error.

***Helix rotula* Hombron & Jacquinot, 1852 (not Lowe, 1831).**

*Helix rotula* Hombron & Jacquinot, 1852 (not Lowe, 1831), Voy. Pol. Sud., Astrolabe et Zélée, Moll., pl. 11, figs. 1–4—Mangareva, Gambier Islands; Rousseau, 1854, Voy. Pol. Sud, Astrolabe et Zélée, Moll., 5, pp. 42–43 (description drawn from figures only); Pfeiffer, 1859, Monog. helic. viv., 4, p. 16.

*Helix (Endodonta) rotula* (Hombron & Jacquinot), Tryon, 1887, Man. Conchol., (2) 3, pp. 67–68, pl. 12, figs. 40–42 (copied from type figures).

*Endodonta (Charopa) rotula* (Hombron & Jacquinot), Pilsbry, 1893, Man. Conchol., (2) 9, p. 35—Name only.

**Remarks.**—The original specimens were apparently lost between the time the figures were prepared and the descriptions written by Rousseau. The figures are of an imperforate, globose, barrier-free shell with relatively prominent reddish flammulations. The form, color, and closed umbilicus immediately suggest *Anceyodonta hamyana* (Ancey) from Mangareva (Solem, 1976b, p. 205, fig. 90a–f), which differs in possessing quite prominent apertural barriers. Either the artist carelessly or deliberately omitted the apertural barriers, the figured shell represents a form of *A. hamyana* now extinct and not found by the Mangarevan expedition, or it is accompanied by erroneous locality data. I suspect the first alternative is more probable, but discussion is purely academic, since the name is preoccupied and no substitute has been proposed.

***Pithys verecunda* Pease, 1870.**

*Pithys verecunda* Pease, 1870, J. de Conchyl., 18, p. 397—Marquesas.

*Pityis verecunda* Pease, 1871, Proc. Zool. Soc. London, 1871, p. 454; Garrett, 1887, Bull. Soc. Malacol. France, 4, p. 16.

*Helix (Pithys) verecunda* (Pease), Pfeiffer, 1876, Monog. helic. viv., 7, p. 257.

*Helix (Endodonta) verecunda* (Pease), Tryon, 1887, Man. Conchol., (2) 3, p. 63.

*Endodonta (Thaumatodon) verecunda* (Pease), Pilsbry, 1893, Man. Conchol., (2) 9, p. 27.

**Remarks.**—The types are not in the collection of the *Journal de Conchyliologie* (J. de Conchyl., 90, p. 76), and their location is unknown. The only specimens labeled as this shell (MCZ 17291, BPBM 170884) are examples of *Libera heyneimanni* from Tahiti. They definitely do not fit the original description and can be presumed to be mislabeled.

The original description suggests a shell similar to the Marquesan *Planudonta subplanula* Solem, *P. intermedia* Solem, *P. concava* Solem, and *P. matauuna* Solem (Solem, 1976b, pp. 335–342, figs. 148–149), but none of the above species matches the apertural barriers of the original description. Until the types can be rediscovered or examples of *Planudonta* that fit Pease's description can be found, the name *Pithys verecunda* must be considered a *nomen dubium*.

## ZOOGEOGRAPHY

In the more than two decades since I published a comprehensive review of the distribution patterns shown by the land snail taxa of the Pacific Basin (Solem, 1959a), the focus of biogeography has shifted drastically. Not only has the concept of "continental drift" become legitimized with the rise of plate tectonics theory and data, but the types of questions asked by biogeographers are different. The equilibrium biogeography of MacArthur & Wilson (1963, 1967), Croizat's vicariance biogeography concepts (see Croizat et al., 1974), the rise of Hennigian cladistic analysis as a research tool, and a shift toward emphasizing species abundance and numbers all have combined to alter the following presentation.

Comparatively little has been published since 1959 concerning the actual distribution of Pacific Basin land snails. The revisions of the Achatinellidae-Tornatellinidae (Cooke & Kondo, 1960, Kondo, 1962) and Endodontidae (Solem, 1976b), a general survey of Australian land snail biogeography (McMichael & Iredale, 1959), a detailed analysis of the New Zealand land snail fauna (Climo, 1975), a study on the species-area relationships of Melanesian land snails by Peake (1969), a discussion of basic land snail distribution patterns (Solem, 1969c), and a brief review of species-area diversity in Polynesian land snails (Solem, 1973e) all provide useful data and ideas.

The analysis presented here is divided into several parts. First, a review of overall distribution patterns at the generic and family levels followed by a brief analysis of the input received from the Pleistocene to Miocene fossils recovered from deep-core drillings. Second, an island group by island group discussion of diversity, emphasizing the extent to which actual specific sympatry has been documented and the probable number of independent colonizations that would be required to derive the known endodontoid fauna of that area. Wherever collecting effort has been inadequate, spread over a period of time in which extinctions have occurred, or has revealed local speciation or an absence of such local diversifications, such data are discussed in detail. Third, general patterns of generic and specific diversity in each archipelago are summarized, and the changing patterns in size as correlated with geography are reviewed. Fourth, a hypothesis as to the origin and diversification of the endodontoid land snail faunas of the Pacific Basin is presented, bolstered by comparative data from other land snail families. Fifth, the general pattern of Pacific Island land snail diversity is

discussed in relation to equilibrium biogeography and species-area theory.

### PATTERNS OF FAMILY AND GENERIC DISTRIBUTIONS

The facts of distribution are relatively simple. The three endodontoid families (fig. 106) have partly overlapping distributions in the Pacific Basin. The most generalized family, the Endodontidae, ranges today in Polynesia from the Ellice Islands and Lau Archipelago east to Henderson Island, the Marquesas, and Hawaii. A disjunct occurrence of one genus, *Aaadonta*, in Palau (Solem, 1976b, pp. 467–487) is partly bridged by the presence of Miocene to Pleistocene fossils on Bikini, Marshall Islands, and Midway Atoll. The Charopidae, which are descended from the Endodontidae, are diverse today in Micronesia (except the Marshall Islands), Polynesia as far east as the Cook and Society Islands, parts of Melanesia (particularly New Caledonia), and extraliminally in New Zealand, eastern and southern Australia, Tasmania, South America, South Africa, and St. Helena. Charopids are found in sharply reduced diversity in the Austral Islands, New Hebrides, Solomon Islands, Bismarcks, New Guinea (Solem, 1958b, 1970a), Northern Australia, and Indonesia (Solem, 1958b). The Punctidae are abundant in eastern and southern Australia, New Zealand, Lord Howe, and Norfolk Islands, with scattered records from New Guinea, Central Australia, the Holarctic region, and Africa (See Verdcourt, 1972, van Bruggen, 1978). In the Pacific Basin proper, there are records from the Society Islands, Austral Islands, and Hawaii. The Punctidae is thus a fringe group within Polynesia.

The pattern of generic distribution is for either very wide or very highly restricted ranges. Very few genera show an intermediate pattern. In the Endodontidae, *Anceyodonta*, *Kleokyphus*, *Opanara*, *Rhysoconcha*, *Ruatarra*, *Orangia*, *Rikitea*, *Kondoconcha*, *Protoendodonta*, *Pseudolibera*, *Gambiodonta*, *Priceconcha*, and *Zyzyxdonta* have single island distributions. *Australdonta* (except for a probable human introduction), *Taipidon*, *Planudonta*, *Nesodiscus*, *Nesophila*, *Endodonta*, and *Aaadonta* have single archipelago distributions. *Libera* is found in the Cook and Society Islands; *Cookeconcha* is extant in the Hawaiian chain, with fossils recorded from Midway and Bikini (fig. 107); *Thaumatodon* has a fairly wide range in Western Polynesia (fig. 107; Solem, 1976b, p. 447, fig. 190); *Minidonta* has a linear range in Eastern Polynesia



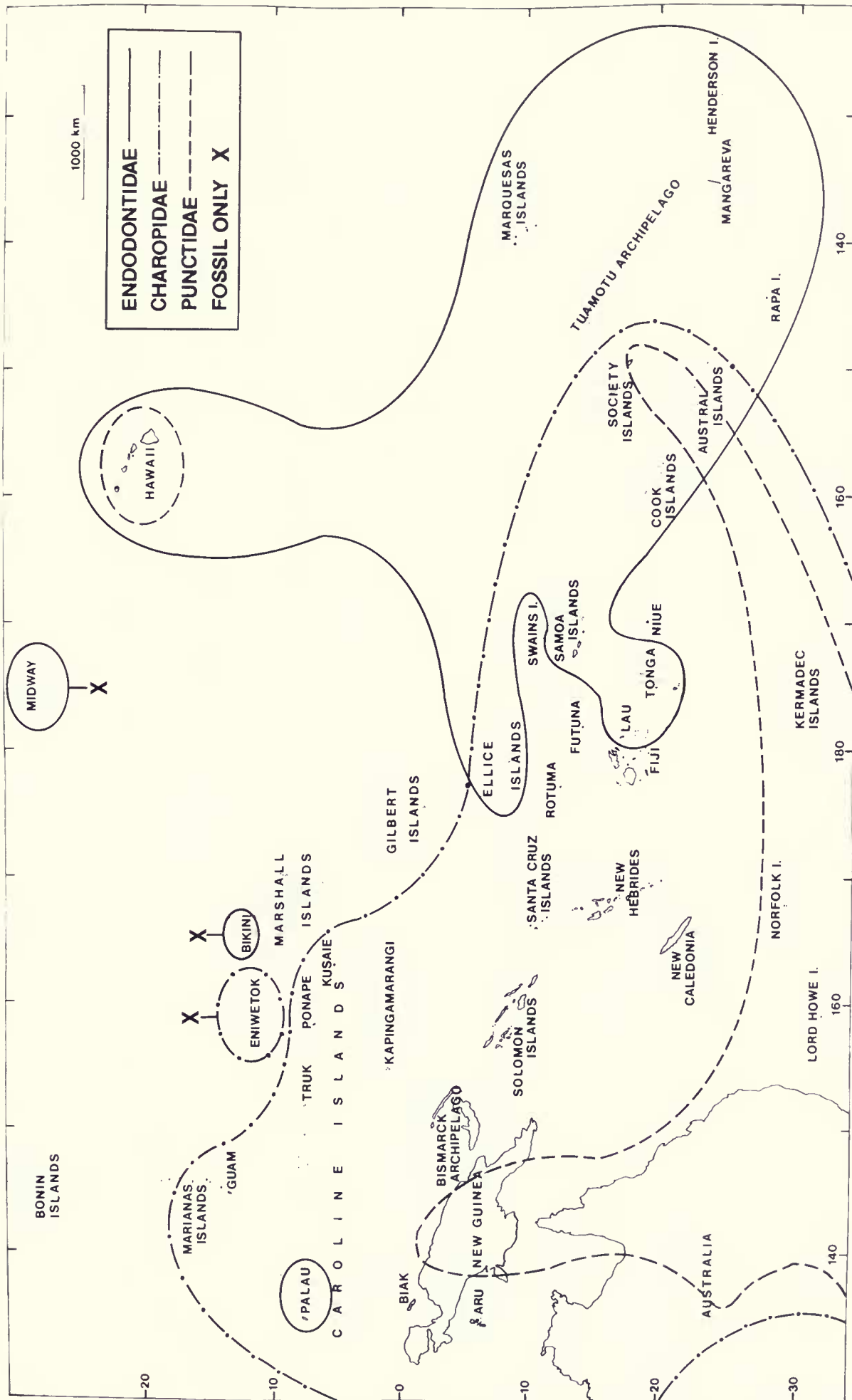


FIG. 106. Distribution of Pacific Island Endodontoid families. Records based only on fossil material are indicated by an "X."

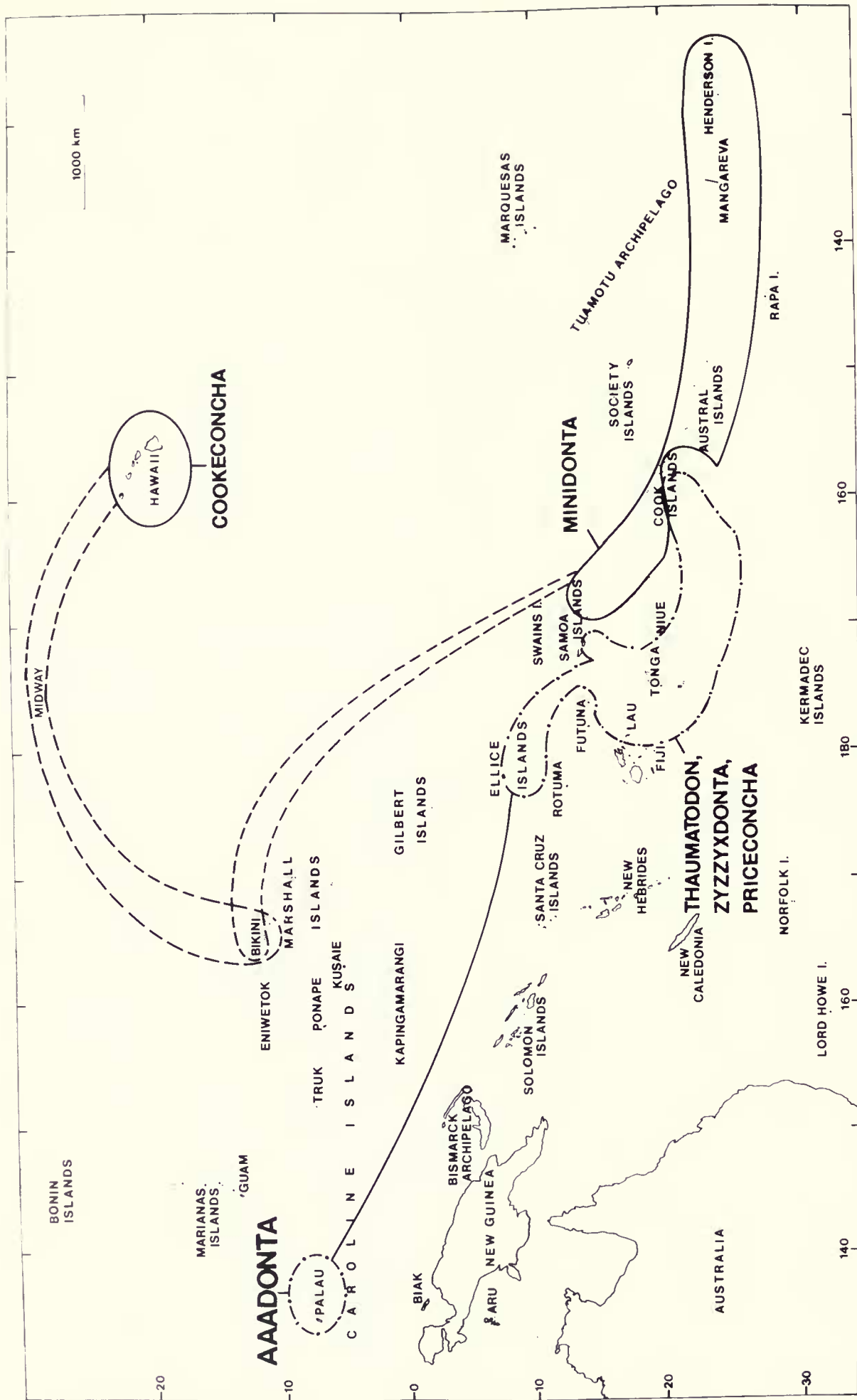


Fig. 107. Distribution of most generalized and most specialized endodontid genera. Range extensions of fossil species in the most generalized genera are indicated by dotted lines.



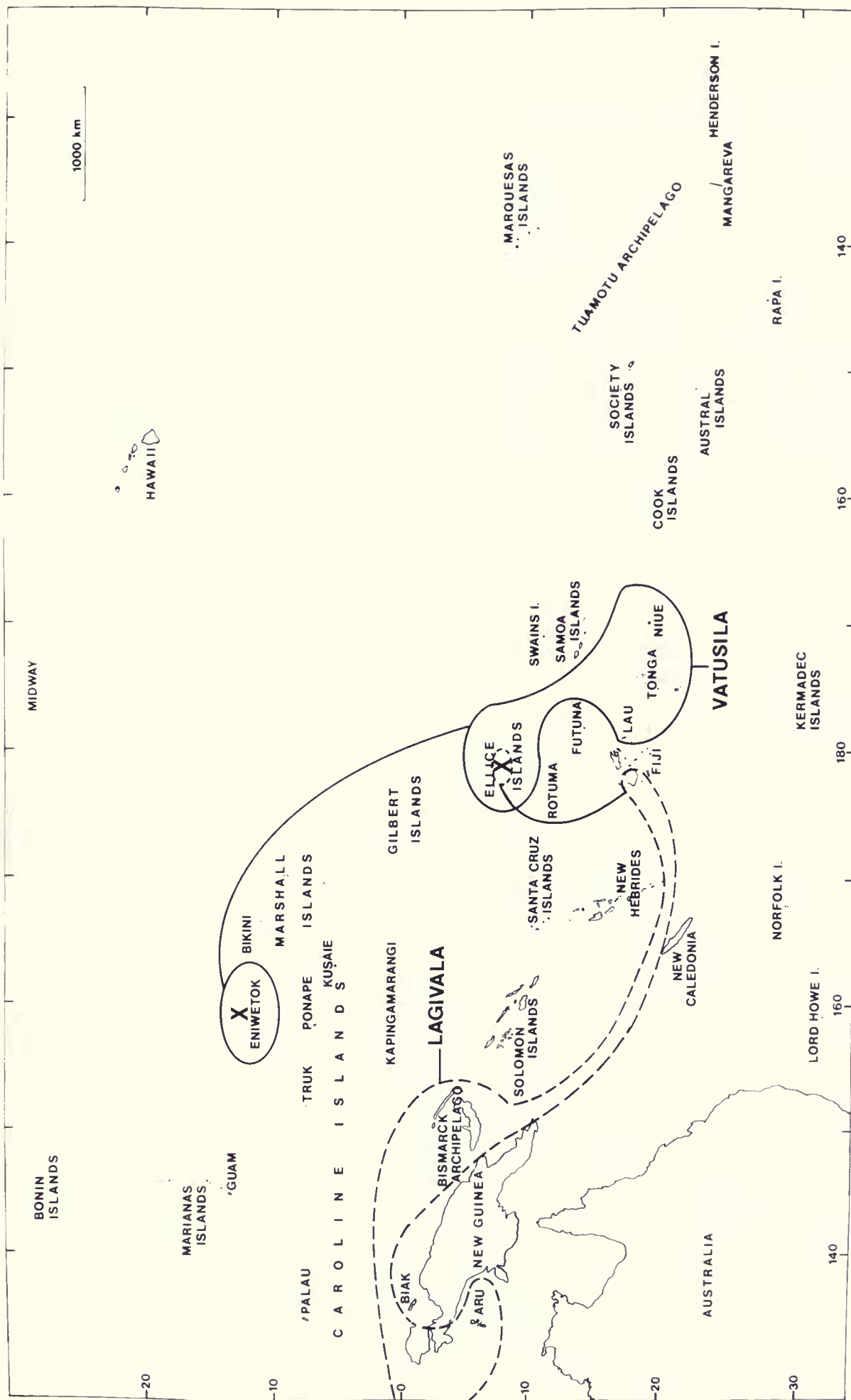


FIG. 108. Ranges of *Lagivala* and *Vatusila*. Range extensions of fossil species are indicated by an "X."

greatly extended northwest by a Pleistocene-Pliocene fossil from Bikini, Marshall Islands; and *Mautodontha* (fig. 109) has a more restricted distribution in Eastern Polynesia. Thus of the 25 endodontid genera recognized, 20 (80%) have a highly restricted range, two (8%) essentially are found in two archipelagos, and only three (12%) have a reasonably wide range. More than half, 13 (52%), are restricted to a single island.

In the Charopidae there are subfamily differences in the degree of generic distributional restriction. In the Micronesian Semperdoninae, *Himeroconcha* and *Ladronellum* are found only on Guam, whereas *Semperdon* has a Palau, Guam, and Rota Islands distribution. In the Trukcharopinae, *Russatus*, *Jokajdon*, *Roimontis*, *Kubaryellus*, and *Palikirus* are restricted to Ponape, *Trukcharopa* to Truk, and only *Palline*, with records from Biak off New Guinea, Palau, and Ponape, shows more than a one-island distribution. The only

Pacific Basin representative of the Rotadiscinae, *Microcharopa*, is recorded from both Fiji and Lau.

In contrast, the genera of the Charopinae tend to have wide distributions. Only *Ba* from Viti Levu, *Lauopa* and *Maafu* from Lau, and *Tuimalila* from Tonga have single-area ranges. *Graeffedon* (fig. 111) occurs in Samoa and Tonga. *Discocharopa* ranges from the Philippines and Indonesia through Northern and Central Australia, Queensland, Bismarcks, New Hebrides, Kermadec, Fiji, Lau, Samoa, Austral and Society Islands; *Vatusila* (fig. 108) has been recorded from Indonesia, west New Guinea and Aru Islands, Bismarcks, and Fiji, with a Pleistocene fossil on Funafuti, Ellice Islands; and *Sinployea* (fig. 110) has Micronesian outliers on Kusaie and possibly Saipan, then a Bismarck to Society Island range, with high diversity in several centers—Tahiti, Rarotonga, Samoa, and Lau. The western limits of *Sinployea* are unknown because

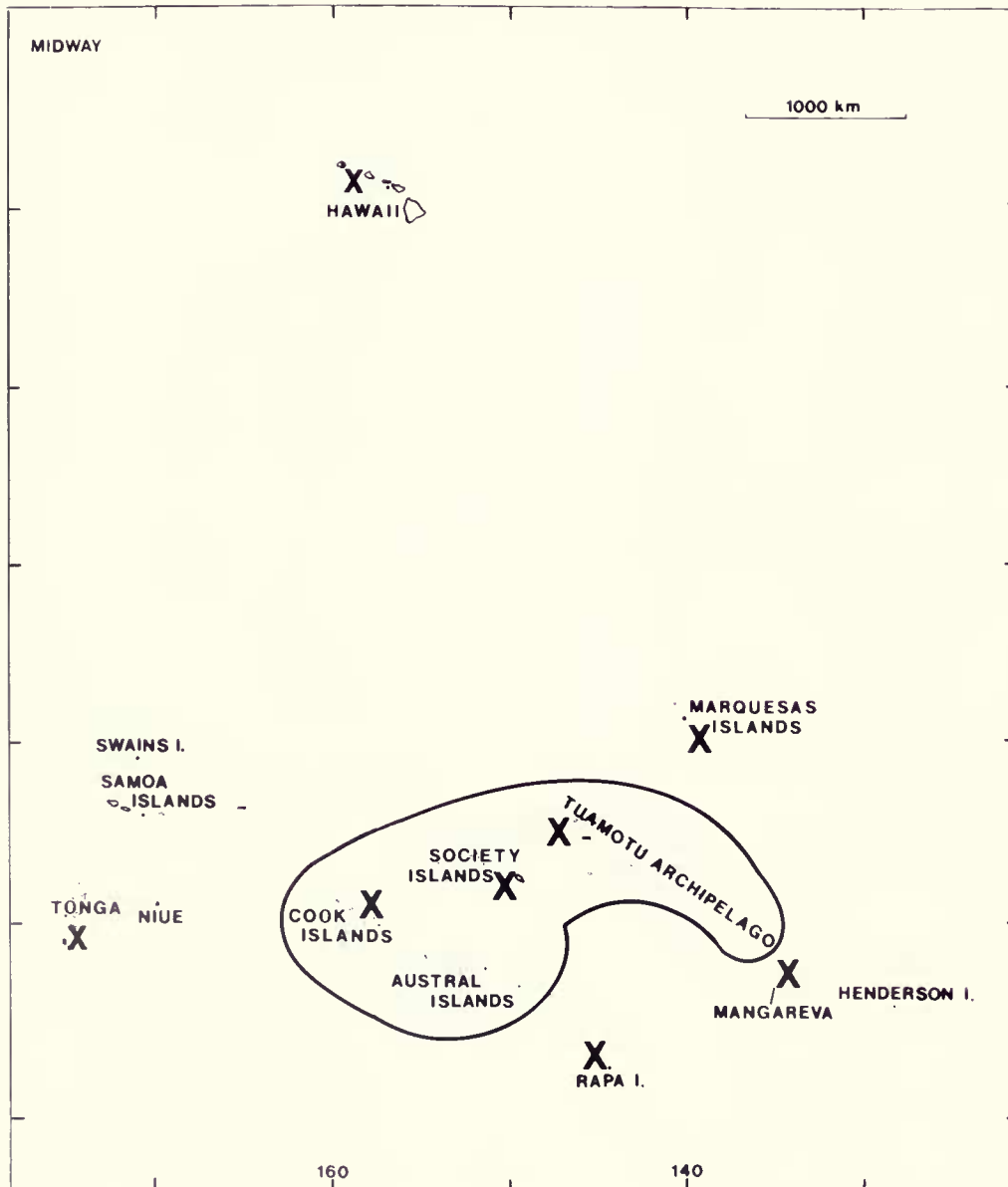


FIG. 109. Range of *Mautodontha* and areas where umbilical brood chambers evolved (X).



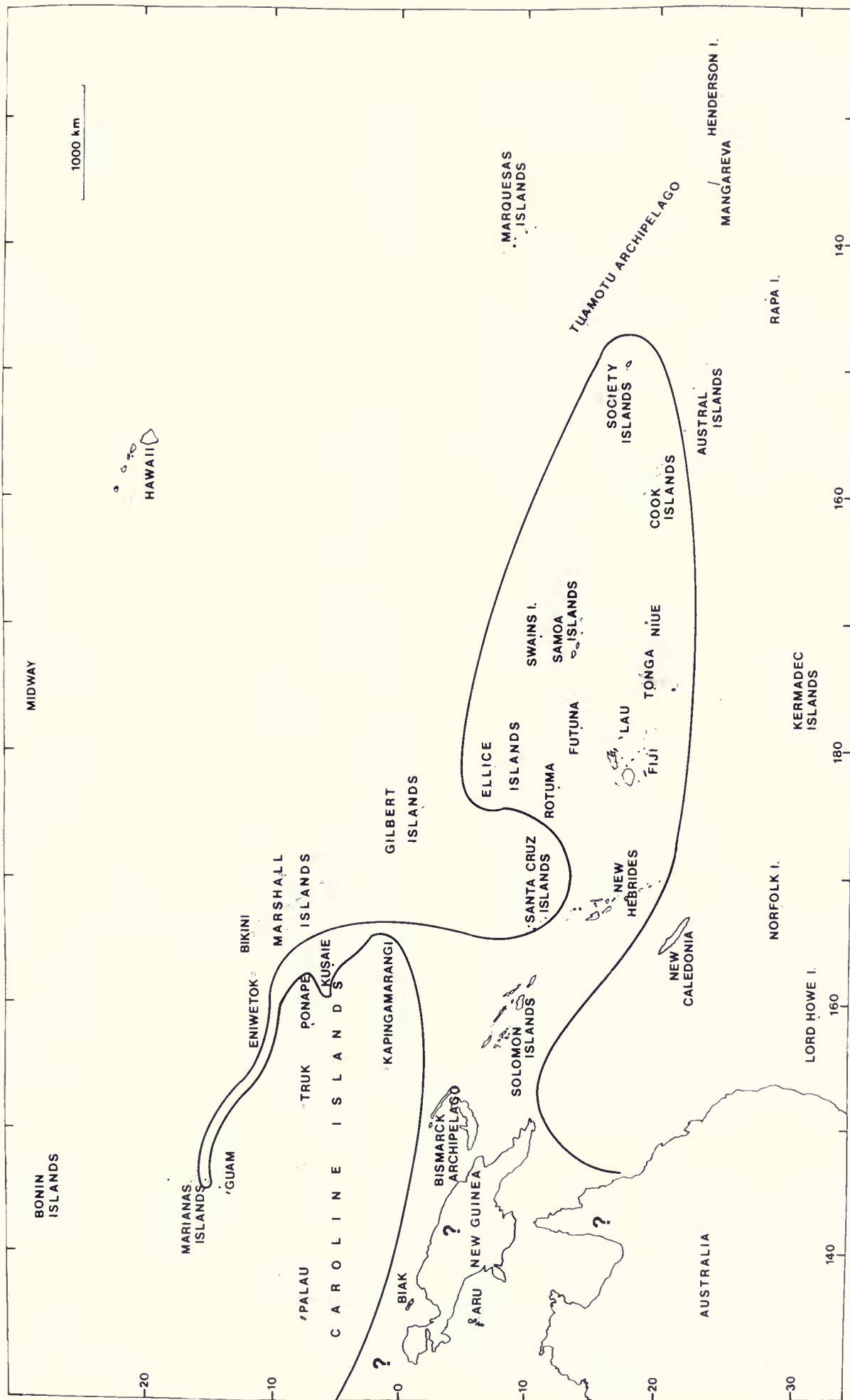


FIG. 110. Range of *Sinployea*. Uncertainty of western limits indicated by question marks and open-ended distribution line.

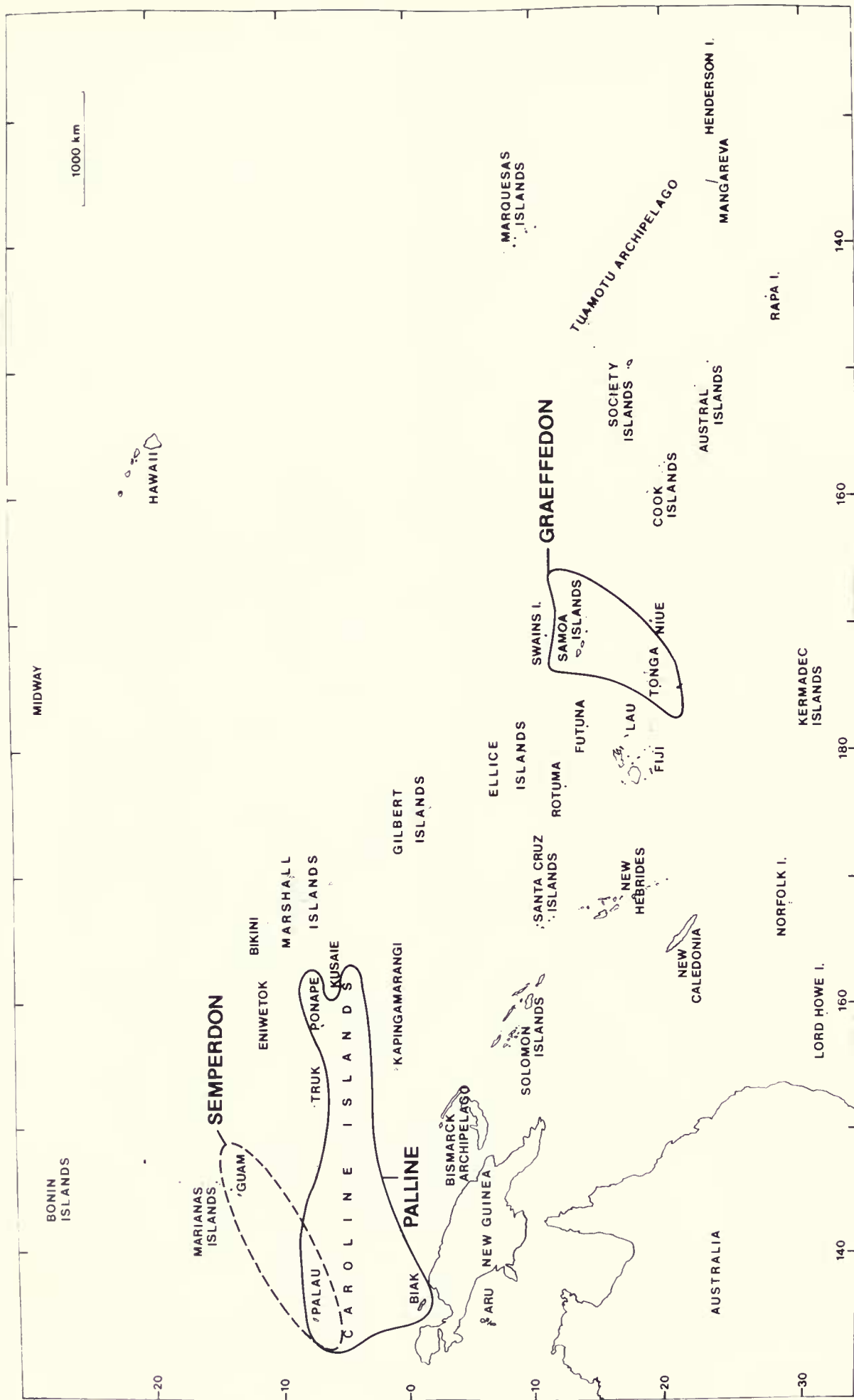


FIG. 111. Ranges of Graeffedon, Palline, and Semperdon.



some New Guinea and Indonesian species assigned to *Pilsbrycharopa* (Solem, 1958b, 1970a) possibly may be misclassified. It is not known if *Sinployea* occurs in Australia, but the New Caledonia *Andrefrancia* (Solem, 1961) is anatomically distinct (Solem, unpublished data). Thus, of the 20 genera recognized in the Charopidae, 12 (60%) have one-area ranges, three (15%) occur in two areas, one (5%) in three areas, and four (20%) are widely dispersed. All of the latter are members of the Charopinae, so that just for the Charopinae, four of nine are widespread, four single area, and only *Graeffedon* has a two-area distribution.

All of the few Pacific Island Punctidae seem to be typical members of the genus *Punctum*, which otherwise is basically a Holarctic taxon. The Australian, New Zealand, Kermadec, Norfolk, and Lord Howe Island Punctidae currently are assigned to a variety of genera. Until Climo finishes his revision of this complex, their actual degree of relationship to *Punctum* will remain unknown.

As shown in Figures 106–108, both the Charopidae and the Endodontidae had wider ranges in the past than they do today. The well-documented Tertiary subsidence of at least 4,500 ft. by Bikini and Eniwetok (see Solem, 1959a, pp. 248, 255, 325–326) has subsequently been confirmed for other areas. For example, Stearns (1978b, pp. 7–9) shows that subsidence of at least 1,000 ft. has occurred in Hawaii since the early Pleistocene, with halts of up to 100,000 years to allow reef building. At the same time, he cited evidence that Lanai had been elevated at least 1,200 ft. during the Pleistocene and that there had been elevational stability in the Hawaiian Islands for the last 500,000–600,000 years. The Central Pacific is thus an area of many and rapid geologic changes. It is evident that Midway, Eniwetok, and Bikini formerly were high islands. The extinction of both endodontids and charopids on these islands was the result of natural processes. As the high islands degraded into atolls, the more frequently interrupted moisture supplies in the litter wiped out the moisture-dependent endodontoid land snails.

Of the Endodontidae, the two most generalized extant genera were found in the core drilling on Bikini. The lower Miocene *Cookeconcha subpacificus* is related to a Pleistocene species from Midway and to extant Hawaiian taxa. The Pliocene to Pleistocene *Minidonta inexpectans* is very closely related to the extant Samoan species, *Minidonta manuaensis*. In the Charopidae, the Upper Miocene *Vatusila eniwetokensis* from Eniwetok is closely related to extant taxa found from the Ellice Islands to Niue. The Pleistocene *Lagivala davidi* from Funafuti, Ellice Islands, is barely distinguishable from an extant Fijian species that occupies the easternmost extension of the generic range. The fact that range contraction rather than range expansion is indicated undoubtedly is an artifact caused by the fact that core sampling has been restricted to atolls in the former areas of high islands, rather than from areas of reef off extant high islands.

At this point, only one additional fact needs to be emphasized. The repetitive evolution of an umbilical brood chamber in Endodontidae from many different areas of the Pacific (fig. 109) represents one of the most unusual aspects of evolution in this group.

#### PATTERNS OF DIVERSITY

Before discussing the details of diversity patterns in relation to contemporary theories concerning species-area relationships and equilibrium biogeography, it is necessary to present a faunistic summary of the endodontoid land snails and details of sympatric occurrences. For convenience, the islands are discussed in rough geographic sequence from East to West, modified only where adjacent archipelagos show clear faunistic affinities that lie outside a strict geographic sequence. The order in which the areas are discussed follows:

- Hawaiian Islands
- Marquesas
- Tuamotu
- Mangareva, Gambier Islands
- Rapa Island
- Austral Islands
- Society Islands
- Cook Islands
- Samoa (both Western Samoa and American Samoa)
- Tonga Islands
- Lau Archipelago
- Fiji, main islands
- Ellice Islands
- Marshall Islands
- Caroline Islands
- Mariana Islands
- Palau Islands

The pattern of treatment is a brief to extended synopsis of collecting history and completeness of faunal survey; where necessary a review of the generic units and number of colonizations involved, a discussion of the extent to which actual sympatric occurrences have been documented, and finally, a review of any clearly defined patterns of intragroup geographic replacement patterns is included. In general, the less satisfactory the material available, the longer the analysis as background to the general summary that follows.

#### Hawaiian Islands

Only a minute fraction of the Hawaiian endodontid fauna has been monographed. Although 30 taxa have been recorded from precise localities in the older literature or in Solem (1976b), there are a much larger number present in collections at the Bishop Museum. Table LXVI summarizes the distribution by genera and Table LXVII, the distribution by island of both species and subspecific units. Table LXVIII presents summary data on all Hawaiian land snails. The basic

TABLE LXVI. - GENERIC DISTRIBUTION OF HAWAIIAN  
ENDODONTIDAE AND PUNCTIDAE

Genus	Recorded	Species in Bishop Museum	% Named
Endodonta	10	79	13%
Cookeconcha	17	100	16%
Nesophila	4	12	33%
Punctum	<u>1</u>	<u>5-9</u>	<u>ca. 14%</u>
TOTALS	32	196-200	16.2%

information for this table is taken from Caum (1928), Neal (1934), Zimmerman (1948), Solem (1976b), and Tables LXVI-LXVII. This information has been used in calculating the geographic comparisons shown in Figures 140-143.

Given the above very incomplete state of taxonomic knowledge, very little can be said concerning sympatry or actual distribution patterns. The following brief historical review hints at the imperfection of knowledge.

The first endodontids known from the Pacific and the Hawaiian Islands were taken during the voyage of the French vessel *Uranie* in the late 1810s. Both *Endodonta lamellosa* (Férussac in Quoy & Gaimard, 1824) and *Cookeconcha contortus* (Férussac in Quoy & Gaimard, 1824) were found among ferns collected on this voyage. Several species, *Cookeconcha stellulus* (Gould, 1844), *C. jugosus* (Mighels, 1845) (plus its synonym *Helix rubiginosus* Gould, 1846, not Johnson, 1964), *C. hystrix* (Pfeiffer, 1846b), and *Nesophila tiara* (Mighels, 1845), were first obtained during the U.S. Exploring Expedition about 1840.

Subsequent material came from resident individuals or from single collectors. A Dr. Frick provided *Endodonta fricki* (Pfeiffer, 1858) and *Cookeconcha hystrixcellus* (Pfeiffer, 1859). The American conchologist Wesley Newcomb collected *Endodonta binaria* (Pfeiffer, 1856) and *E. apiculata* Ancey (1889). W. Harper Pease (1866, 1870) described six species, *Nesophila distans*, *N. capillata*, *Endodonta rugata*, *E. laminata*, *Cookeconcha decussatulus*, and *C. paucicostatus*, but

TABLE LXVII. - GEOGRAPHIC DISTRIBUTION OF SPECIES LEVEL TAXA IN  
HAWAIIAN ENDODONTIDAE

Islands	Recorded or Described	Taxa Present in Bishop Museum	
		Species	Races and Varieties
Kauai	10	29	28
Niihau		5	
Oahu	8	107	77
Molokai, Lanai, Maui	10	41	11
Hawaii	<u>6</u>	<u>9</u>	<u>4</u>
TOTALS	34	191	120

TABLE LXVIII. - DIVERSITY OF HAWAIIAN LAND SNAILS

FAMILY	ISLAND					
	Kauai	Oahu	Maui	Lanai	Molokai	Hawaii
Hydrocenidae	1					
Helicinidae (Neal, 1934)	10	5	2	1	2	2
"Pupillidae"	10	25	15	7	14	26
Achatinellidae						
Partulina		2	33	3	22	3
Achatinella		42				
Tornatellininae	8	45	22	2	18	19
Amastriidae						
Leptachatina	23	58	18	8	15	9
Carelia	10					
Pterodiscus		6		1		
Planamastra		1				
Armsia		1				
Amastra	11	60	28	10	24	17
Laminella		3	5	3	3	
Succineidae	6	7	7	2	4	21
Subulinidae	2	5	2		2	4
Helicidae	1	1	1	1	1	1
Zonitidae & Helicarionidae	16	27	14	7	9	17
Endodontidae	<u>29</u>	<u>107</u>	<u>ca. 20</u>	<u>ca. 9</u>	<u>ca. 12</u>	<u>9</u>
TOTALS	127	395	167	54	126	128

whether these were self-collected or, more probably, provided him by others is unknown. C. F. Ancey (1889) summarized previous knowledge, described one species (*C. elisae*) that may not be Hawaiian, and another (*N. baldwini*) received from John H. Thomson that purportedly originated from the U.S. Exploring Expedition material. Later, Ancey (1899, 1904) published new species collected by Ditlev Thaanum (*Cookeconcha nudus*), H. W. Henshaw (*C. henshawi*), and Rev. Thwing (*C. thwingi*). Sykes (1896) distinguished two new species, *Cookeconcha ringens* and *C. lanaiensis*, among materials gathered by R. C. L. Perkins for the "Fauna Hawaiiensis." Pilsbry & Vanatta (1905, 1906) named five species assembled from a number of sources (*Endodonta kamehameha*, *E. concentrata*, *E. marsupialis*, *Cookeconcha luctiferus*, and *C. thaanumi*). Finally, T. D. A. Cockerell (1933) described a single species that he collected on Oahu.

Nondescriptive studies are minimal. D. D. Baldwin (1893) provided some locality records in his privately printed *Catalogue, Land and Fresh Water Shells of the Hawaiian Islands*. Sykes (1900) summarized previous literature citations, added locality records that are mostly based on too broad an interpretation of species limits, and provided some notes on variation. Pilsbry & Vanatta (1906) gave limited data on ecology in *Endodonta* and *Cookeconcha*. Cooke (1928) gave detailed information on anatomy, varia-



tion, and historical references for the three Oahu *Endodonta* that had been previously described. A general checklist of Hawaiian shells was prepared by Caum (1928).

It is obvious from the above account that published data is based on essentially incidental observations. From 1900 on, however, the late C. M. Cooke, Jr., and several amateur collectors amassed about 5,800 sets of Hawaiian endodontids in the Bernice P. Bishop Museum. At least 50,000 specimens and probably 300 morphologically distinguishable entities (local variations, subspecies, and species) are represented. Until this material is reviewed, no statements concerning the distribution of Hawaiian endodontids will have any meaning. The systematic review presented earlier (Solem, 1976b, pp. 207–224, 365–368, 371–383), which was intended only to survey patterns of variation and to relate the Hawaiian taxa to other endodontid genera, was based on only 238 shells of 25 species, plus dissection of six named species and two undescribed taxa.

Of the three endodontid genera recognized, *Cookeconcha* is the most generalized, with the *C. henschawi* complex forming a group on the same evolutionary level as *Minidonta*. The other species groups in *Cookeconcha* show increased size, progressive loss of apertural barriers, and apical sculpture, but retain their postnuclear radial sculpture and a rounded periphery. At least some species will live in moss or under bark above ground level. *Endodonta* is a conchologically specialized derivative of *Cookeconcha*, with a strong tendency toward loss of sculpture, development of a markedly protruded keel, retention of large apertural barriers, and a strictly terrestrial habitat. *Nesophila* is derived from *Cookeconcha*, but shows specialization in loss of all columellar and palatal barriers, splitting of the parietals into many threadlike traces, and distinct shouldering of the umbilical margin. Anatomical variation in the dissected *Cookeconcha* is large, and the genus is more broadly defined than others utilized in this study. Probably it will be subdivided into at least two or three genera when the Bishop Museum material is studied in detail. The fossil taxa from Midway (Solem, 1977a) include a generalized *Cookeconcha* and a new genus, *Protoendodonta*, that is partly transitional to *Endodonta*.

Superficial examination of unstudied material in the Bishop Museum does permit a few observations. More than on any other island or island group in the Pacific, the Hawaiian endodontids show a wealth of minor variations between populations, many of which should not even be considered subspecific. Whereas nearly all the Endodontidae from Polynesia showed only extremely minor variation between populations within a species or subspecies, the Hawaiian material shows extensive variation. Part of this may be caused by the dissected topography and strong rain shadow effects of island orientation. Of equal importance, the present main islands of Hawaii are young in compari-

son with islands such as Saipan or Rapa. Thus the Hawaiian endodontids, as the Hawaiian achatinellids, should be viewed as a group undergoing explosive speciation, with many forms only partly differentiated. Because the endodontids show many more conchological features than the achatinellids and tornatellinids, I believe that they offer extremely productive material for the study of microevolution. Analysis of speciation and variational patterns in the Waianae endodontids, for example, would be highly interesting and would yield much more data per sample than the *Achatinella*.

Unfortunately it may even now be too late for maximum usefulness. At best, endodontids remain only along the crest of the Waianae Range, with the invasions of introduced ferns, grasses, and ants having exterminated the populations at lower levels. *Endodonta* is restricted to the ground stratum and, as with most Endodontidae, becomes extinct whenever any disturbance of the vegetation occurs. *Cookeconcha* may tolerate a somewhat greater degree of disturbance and possibly still can be collected in larger patches of native vegetation. Traces of *Cookeconcha* were seen in 1961 in relatively small patches of native plants in the Waianae Mountains and on Kauai, but no signs of *Endodonta* were encountered.

Unlike the achatinellid-tornatellinid and amastrid complexes, the Hawaiian endodontids show no obvious pattern of island speciation. Such indications as may be inferred from the dribblets of material reported on previously are immediately disproved by examination of the Bishop Museum material. Hence, no discussion of local distribution is attempted, except to note the apparent restriction of *Nesophila* to Kauai and the relative absence of endodontids in the Koolau Range of Oahu (less than a dozen colonies known) compared with their fantastic abundance in the Waianae Mountains. The very small species representation on Hawaii, Lanai, and Molokai in comparison with the great abundance in the Waianae Range and moderate abundance on Kauai apparently is real and not an artifact of collecting efforts. Because the former islands are significantly younger in age than the latter, although the exact datings still remain controversial, it is intriguing to speculate whether the increased diversity on Kauai and Oahu represents a simple factor of longer time available for diversification or whether biotic factors have prevented diversification on the younger islands. No data are available concerning the latter possibility, but the above point will be referred to later.

The Hawaiian radiation probably is a monophyletic one.

### Marquesas Islands

Endodontoid land snails were collected during three periods. Garrett in the 1860s (?) and 1880s; the B. P. Bishop Museum Pacific Entomological Survey in 1929–1932, plus a single specimen collected by Quayle in 1922; and some specimens taken on Eiao by John

Peake in 1970. There is almost no overlap among the collections, with the species collected by Garrett—*Taipidon analogica* (Pease, 1870), *T. octolamellata* (Garrett, 1887), *T. woapoensis* (Garrett, 1887), *T. anceyana* (Garrett, 1887), and *T. marquesana* (Garrett, 1887)—not being known from later collections. Only one of these, *Taipidon woapoensis*, was reported from moderate (2,000 ft.) elevation.

Most material collected by the Pacific Entomological Survey was taken "... on the ground among dead leaves, in the cloud zone" (Adamson, 1935, p. 32), generally at elevations above 3,800 ft., although *Taipidon varidentata* was taken as low as 2,600 ft. on Hivaoa. One specimen of *Planudonta subplanula* was collected in 1922 by Quayle on the Tovii plain of Nukuhiva at about 200 ft. elevation. The apparent restriction of endodontids to high elevations undoubtedly reflects the fact that by 1932 "The native flora below 1,000 feet has been replaced in large measure by immigrants, and to a considerable extent up to 2,500 feet" (Adamson, 1936, p. 42). With the essential limitation of Endodontidae to undisturbed forest areas, undoubtedly the species collected by Garrett are now extinct. Although no such data accompanied the actual specimens in the Bishop Museum, apparently *Taipidon petricola* "was found in large numbers under bark on Eiao and Hatutu" (Adamson, 1935, p. 32). Whether this involved fallen logs or stilt roots is unknown. Persistence in semidisturbed areas becomes possible, and the record of *Taipidon petricola petricola* from a coconut plantation area of recent planting (Solem, 1976b, p. 323) becomes less unusual.

Only 186 specimens of 15 species were seen, proportionately the smallest amount of material available for this study from any major archipelago. Although the Pacific Entomological Survey covered most of the islands (Adamson, 1935, pp. 3–6), analysis of the collecting records for endodontids indicate that the visits of Adamson to Nukuhiva, Hivaoa, Eiao, and Hatutu in 1929 and early 1930 account for nearly all the specimens. Only a few specimens of *Taipidon fragila* and *T. varidentata* were taken by LeBonnec in late 1930 and at the very end of his fieldwork in early 1932. Hence, the absence of endodontids from the Pacific Entomological Survey collections on Uapou, Uahuka, Tahuata, Fatuuku, Fatuhiva, and Mohotani probably reflects LeBonnec's concentration on insects and failure to explore the ground stratum in a way that would obtain endodontids. Since Adamson spent only a single day on Mohotani (Adamson, 1935, p. 5), lack of material from this island has no significance.

Under the circumstances outlined above, it is evident that only a small part of the Marquesas was explored for endodontids. With the great destruction of the native forests already present by 1930, the probability of obtaining lowland specimens is remote. Peake found no specimens at high elevation in 1970 (personal communication). Unless the introduced ants have reached very high elevations, I consider the possibility

of collecting endodontids in forest fragments on the peaks of Fatuhiva, Tahuata, Uapou, and Uahuka excellent and expect that additional species can be found on both Hivaoa and Nukuhiva. Until further attempts at exploration have been made, no statements of distributional patterns within the archipelago will have any validity. Single species are known from Hatutu (*Taipidon petricola petricola*), Eiao (*T. petricola decora*), and Uapou (*T. woapoensis*). *Taipidon analogica* (Pease, 1870) is not known from an exact locality. No species have been reported from Uahuku, Fatuhiva, Tahuata, Mohotani, or Fatuuku.

More material is known from Hivaoa and Nukuhiva. The six species reported from Nukuhiva are:

*Taipidon marquesana* (Garrett, 1887)  
*T. semimarsupialis* Solem  
*T. centadentata* Solem  
*Planudonta subplanula* Solem  
*P. intermedia* Solem  
*P. concava* Solem

The five species reported from Hivaoa are:

*Taipidon anceyana* (Garrett, 1887)  
*T. octolamellata* (Garrett, 1887)  
*T. fragila* Solem  
*T. varidentata* Solem  
*Planudonta matauuna* Solem

Garrett's species presumably were taken at lowland stations and almost certainly are extinct. The remaining species collected between 1929 and 1932 probably still could be found at very high elevations.

Two genera have been recognized—*Taipidon* and *Planudonta*. The latter is characterized by its depressed spire, altered pattern of coiling, and umbilical sculpture; the former shows several incipient trends that, if more adequate material had been available, might have resulted in subgeneric or even generic recognition. *Planudonta* is known from both Nukuhiva and Hivaoa, at high elevations, except for a single subadult taken in 1922 on the Tovii plain at about 200 ft. elevation.

*Taipidon* is known from all Marquesan islands from which endodontids have been recorded. The polytypic *T. petricola* from the northern islands of Hatutu and Eiao shows similarities to *Mautodontha* (*Garrettoconcha*) in apertural barriers and lack of a fleshy extension to the penis head, but the presence of strong secondary spiral cording, more widely spaced and few ribs, unequal-sized penial pilasters, and the pustulose zone in the penis (Solem, 1976b, p. 85, fig. 49b) are characters shared with the other *Taipidon* and are very different from the characters seen in the Society Island group. Whether *T. petricola* is primitively small or secondarily small is unknown. Its anatomy shows no sign of secondary size reduction, but this is the smallest species in which the penial retractor originates from the columellar retractor. Species similar to *T. petricola* include all those collected by Andrew



Garrett. They show combinations of minor variations: three (*T. woapoensis*, *T. octolamellata*, *T. marquesana*) or two (*T. anceyana*, *T. analogica*) parietals; a V-shaped and wider (*woapoensis*, *anceyana*, *marquesana*) or U-shaped and narrower (*octolamellata*, *analogica*) umbilicus; presence of strong (*analogica*), weak (*octolamellata*, *anceyana*), or no (*marquesana*, *woapoensis*) secondary spiral cording; an absent or weak (*marquesana*, *woapoensis*), typical (*analogica*), or prominent (*anceyana*, *octolamellata*) columellar barrier; high (*analogica*) or relatively low (others) spire. The general facies of these species is the same. Despite the numerous accessory traces, smaller size, and four parietals of *T. petricola*, this seems a monophyletic assemblage.

On Hivaoa *T. varidentata* and *T. fragila* differ in their greatly crowded and fine sculpture, variable number of palatal barriers that are crescentic and clustered in some individuals, inflated appearing body whorl, very thin shell, relatively short and fat penis (Solem, 1976b, p. 320, fig. 138e, g), compact prostate-uterine region, and slender parietals. To the extent that available specimens permitted study, their anatomy differs only in degree from that of the other *Taipidon*, but many features could not be examined. The differences cited above are large and structurally uncorrelated. Subgeneric or generic recognition may be advisable if and when adequate material can be studied.

On Nukuhiva *T. centadentata* and *T. semimarsupialis* diverge from the basic pattern. Conchologically, they are quite dissimilar, *T. centadentata* having numerous short columellar and palatal traces on a raised callus and 15 to 20 parietal traces. Although relatively large in size and with prominent secondary spiral cording, the shell shape and umbilical form do not differ from the *petricola* series. *Taipidon semimarsupialis* has the umbilicus altered to form a brood chamber by gradual inward growth of the last whorl and a quarter. This is accompanied by marked increase in H/D ratio and whorl count, but the ribbing and apertural barriers show that this is a development from the *petricola* complex. Although the jaws of both species are partly fused, probably a simple correlative of their size, their radulae are characterized by larger numbers of comparatively small teeth—13 to 15 laterals in *semimarsupialis*, 22 to 23 laterals in *centadentata*; 10 to 13 and 16 to 17 marginals, respectively. Since all other Endodontidae have only 6 to 10 laterals and 7 to 10 marginals, this change is dramatic. Possibly, it may reflect a dietary alteration.

Meager evidence (Solem, 1976b, p. 317) suggests that *T. varidentata* and *T. fragila* may be altitudinal replacements, the former from lower elevations. Without more concentrated collecting effort, the reality of the recorded altitudinal zonation cannot be accepted on face value.

Patterns of diversity cannot be determined from available data. On both Nukuhiva and Hivaoa Islands,

two or more species are sympatric, and their anatomies show evidence of species recognition character displacement in the terminal genitalia (Solem, 1976b, pp. 79, 81–82). The few records are summarized below for convenience. This radiation, despite its conchological diversity, appears to be monophyletic.

#### NUKUHIVA ISLAND

Puokoko on Tunoa Ridge, cloud zone at 3,485 ft. elevation. October 22, 1929.

*Planudonta subplanula* Solem—1

Tovii region, at 200 ft. elevation. October, 1922. Collected by Quayle.

*Planudonta subplanula* Solem—1

Mt. Ooumu, ridge at 3,900 ft. elevation, on damp ground among leaves and other debris. November 13, 1929.

*Taipidon centadentata* Solem—43

*Planudonta concava* Solem—1

Mt. Ooumu, near summit at 4,050 ft. elevation, among leaves and wet humus. November 12, 1929.

*Taipidon semimarsupialis* Solem—3

*Taipidon centadentata* Solem—13

*Planudonta intermedia* Solem—1

#### HIVAOA ISLAND

Mt. Temetiu, crest to north of trail, at 2,615 ft. elevation. July 24, 1929.

*Taipidon varidentata* Solem—1

Matauuna Valley, north of Mt. Temetiu's summit, at 2,800 ft. elevation, under dead leaves on ground. February 26, 1930.

*Taipidon varidentata* Solem—1

Same as above at 3,800 ft. elevation. February 4, 1930.

*Taipidon varidentata* Solem—1

*Planudonta matauuna* Solem—1

Mt. Temetiu, ridge at 3,860 ft. elevation, on dead leaves. December 27, 1930.

*Taipidon varidentata* Solem—1

Mt. Temetiu ridge, 4 km. from shore, at 3,950 ft. elevation, on dead leaves. December 12, 1929.

*Taipidon fragila* Solem—2

Same at 4,160 ft. elevation. January 22, 1932.

*Taipidon fragila* Solem—1

Feani Ridge, Tenatinaei at 3,905 ft. elevation in moss. February 19, 1932.

*Taipidon fragila* Solem—7

#### Tuamotu Archipelago

Except for the scattered collections of *Mautodontha daedalea* (Gould, 1846) from the atolls of Anaa and Niau, all known endodontids are from the raised coral island Makatea. Cooke (1934) summarized the previous history of collecting from this island and recorded a total of 22 land snail taxa, including *Mautodontha daedalea* and the specimen referred to as "Liberia species" that subsequently became the holotype of *Pseudolibera lillianae* Cooke & Solem, 1976 (Solem, 1976b, pp. 383–385, fig. 168a–b). Aubert de la Rüe & Soyer (1958), in a curiously flawed paper, reported a number of Society Island endodontids from Makatea. Restudy of these resulted in the description of a second endemic genus with two species. *Kleokyphus callimus* Solem, 1976, and *K. hypsus* Solem, 1976 (Solem, 1976b, pp. 224–227, fig. 95a–f), plus a juvenile individual of *Pseudolibera lillianae*. Subsequently, during a visit to the Paris Museum, it

was discovered that the material which Aubert de la Rüe & Soyer (1958) had reported as the helicarionid "*Trochonanina obconica* Pease" was a mixed lot containing one example of *Liardetia* (*Oceanesia*) *discordiæ* (Garrett, 1881), several examples of *Pseudolibera lillianæ*, plus the three new species of *Pseudolibera* Solem (in preparation B). There are thus a total of seven endodontids known from Makatea. *Mautodontha daedalea* also has been reported from Anaa and Niau, but *Kleokyphus* and *Pseudolibera* represent endemic genera. *Kleokyphus* is a direct derivative from *Mautodontha*, whereas *Pseudolibera* is a development that precisely parallels the Society Island *Libera*.

There are no data concerning the degree of sympatric occurrence among these taxa. Because they apparently are relatively abundant in coralline deposits, a study on at least fossil distributions would be feasible and worthwhile.

I am uncertain whether this is a monophyletic or diphyletic radiation.

### Mangareva, Gambier Islands

The primary goal of the Bishop Museum Mangarevan Expedition in 1934 was to obtain living land snails from Mangareva. The material described by Pfeiffer (1845) and Ancey (1889) as *Anceyodonta sexlamellata* and *A. hamyana*, respectively, was not localized as to islet and could not be so assigned during this study.

During the Bishop Museum Expedition, considerable time was spent on Mangareva and Aukena Islets with comparatively little time spent on Taravai and Agakauitai. From the original field maps, which were based on available French charts, collecting localities on the smaller islets (fig. 112) and on Mangareva (fig. 113) have been presented. No living material of endodontids was obtained, but specimens proved to be quite abundant in several cave deposits or road cuts. A total of 25 species and subspecies, varying in abundance from one to 577 specimens, was obtained (Solem, 1976b, p. 185, table LXXI). Because of the remarkable nature of this radiation, the closeness of localities in several instances, and the probable high localization of species within particular deposits, full data on species diversity is being presented below.

Of the three endemic genera, *Anceyodonta* intergrades and is derived from the widely distributed *Minidonta*; *Rikitea* is an independent evolution of the *Nesodiscus*-level of specialization; and *Gambiodonta* is a local achiever of the brood chamber level of specialization that is directly derivable from *Anceyodonta*. Conceivably they could originate from only two or three colonizations.

Questions of local diversity require additional material and analysis. As pointed out by Solem (1976b, pp. 184–186, table LXXII), stations within 100 to 300 ft. of each other differed significantly in their species composition. Since the collectors were primarily interested in another family, the species are small and

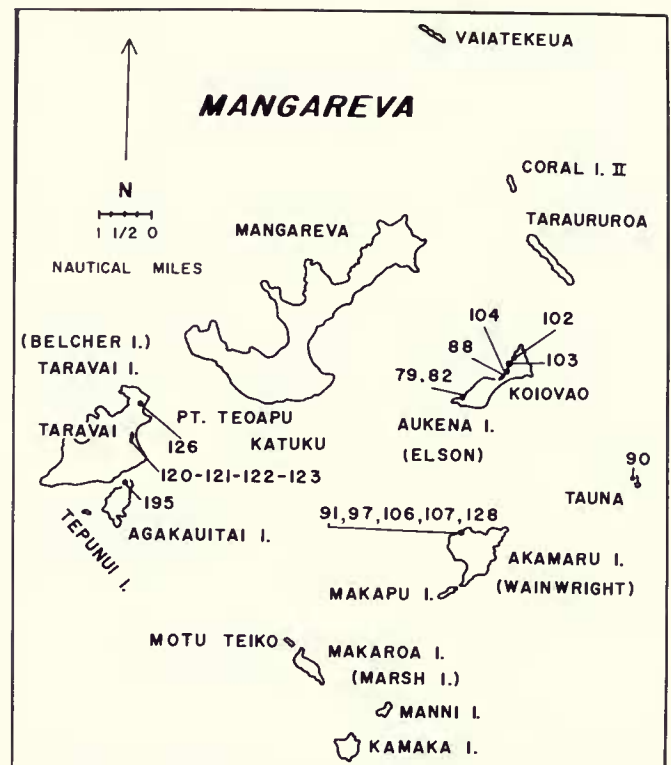


FIG. 112. Collecting localities on smaller islets of Mangareva, Gambier Islands. Mangarevan Expedition, 1934.

look very similar to the naked eye, and a conscientious effort to "get everything" was made, I reject collection bias as a factor in the known diversity. Collecting effort was definitely not equivalent at each station. However, levels of species diversity are quite interesting. On Aukena Islet, six species were taken at Stations 82 and 103, seven species at Station 87, and nine species at Station 102. On Taravai, four species were taken at Station 126. The greatest diversity was found on Mangareva itself, with seven species at Stations 195 and 197, nine species at Stations 142 and 189, 10 species at Station 187, and 12 species at Station 277. Since only 12 species were found on Aukena, five on Taravai, and 17 on Mangareva, the degree of sympatry apparently reached the minimum of 75% on Aukena, 80% on Taravai, and 71% on Mangareva. Within a single genus, three to four species of *Anceyodonta*, three species of *Minidonta*, and three species of *Gambiodonta* were sympatric on Aukena, and up to nine species of *Anceyodonta* were sympatric on Mangareva.

Several times in recent years, I made various fiddlings with indices of species abundance using the Mangarevan data, but without reaching any significant conclusions. For the benefit of the more mathematically inclined, the full data on relative abundance and station occurrence follows.

Station 79, hillside, western end Aukena Islet, on dead leaves under coconut trash. S. Wight and Yoshio Kondo. May 27, 1934.

*Anceyodonta sexlamellata* (Pfeiffer)—2

Station 82, flat area of 10 ft. elevation, 20 ft. inland, by side of trail, west end Aukena Islet. D. Anderson and C. M. Cooke, Jr. May 28, 1934.



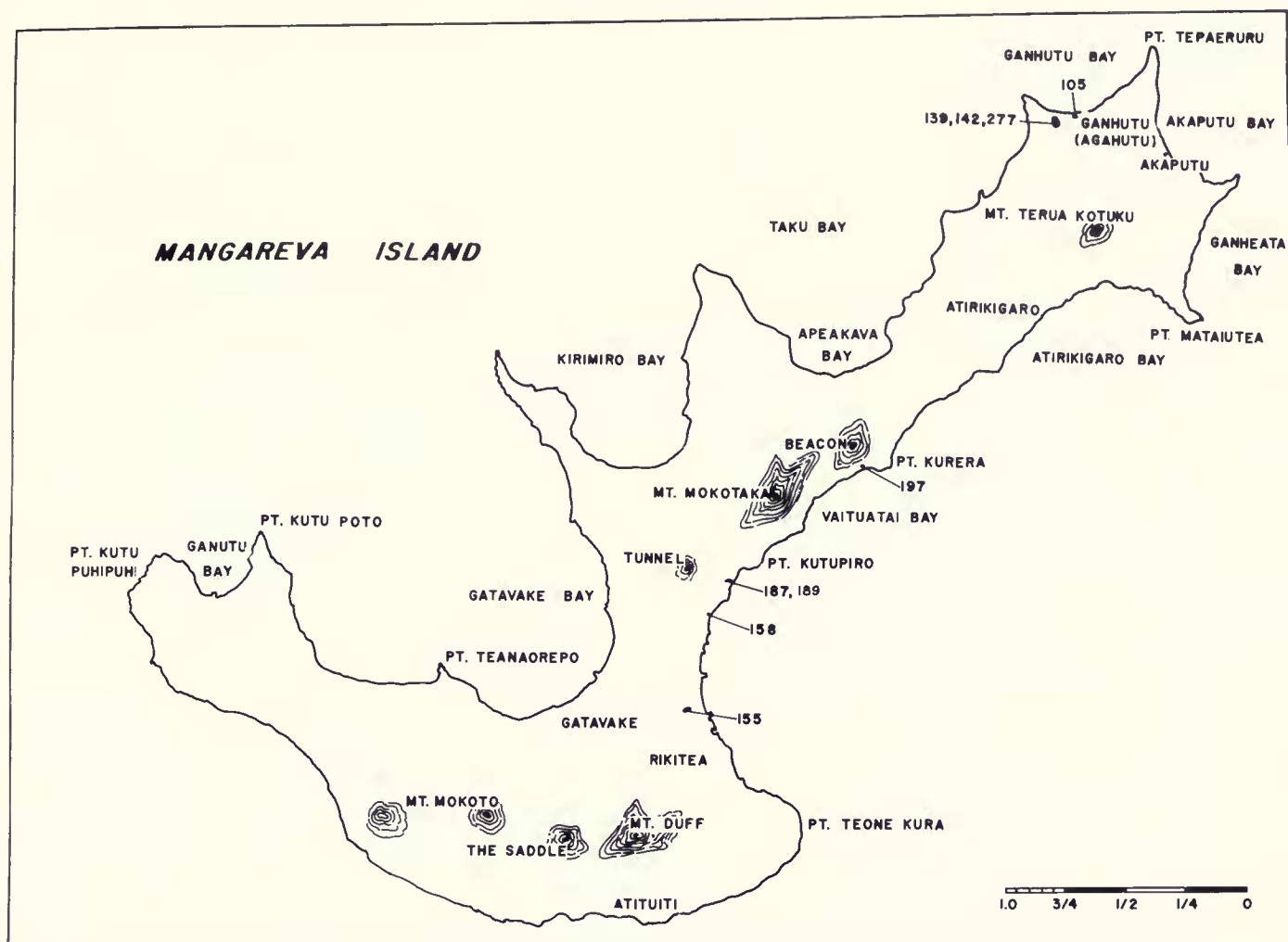


FIG. 113. Collecting localities on Mangareva Islet, Mangareva, Gambier Islands. Mangarevan Expedition, 1934.

- Anceyodonta sexlamellata* (Pfeiffer)—6  
*Anceyodonta obesa* Solem—1  
*Anceyodonta hamyana* (Ancey)—101  
*Gambiodonta pilsbryi aukenensis* Cooke & Solem—1  
*Gambiodonta mirabilis* Cooke & Solem—2  
*Gambiodonta grandis* Cooke & Solem—11  
 Station 88, flat area 100 ft. inland, at 6 ft. elevation along trail near gap, Aukena Islet. D. Anderson and C. M. Cooke, Jr. May 28, 1934.  
*Anceyodonta labiosa* Solem—25  
*Anceyodonta obesa* Solem—222  
*Anceyodonta hamyana* (Ancey)—40  
*Gambiodonta pilsbryi aukenensis* Cooke & Solem—76  
*Gambiodonta grandis* Cooke & Solem—197  
*Gambiodonta mirabilis* Cooke & Solem—2  
*Minidonta simulata* Solem & Cooke—19  
 Station 97, flat area, 20 to 200 ft. inland at 6 ft. elevation, on cliffs, northwest side of Akamaru. D. Anderson. May 28, 1934.  
*Anceyodonta sexlamellata* (Pfeiffer)—18  
*Anceyodonta obesa* Solem—3  
*Anceyodonta labiosa* Solem—2  
 Station 102, first cave east of gap, Aukena Islet. D. Anderson. May 28, 1934.  
*Anceyodonta subconica* Solem & Cooke—61  
*Anceyodonta sexlamellata* (Pfeiffer)—128  
*Anceyodonta obesa* Solem—73  
*Anceyodonta hamyana* (Ancey)—20  
*Gambiodonta pilsbryi aukenensis* Cooke & Solem—1  
*Gambiodonta grandis* Cooke & Solem—18  
*Minidonta micra* Solem & Cooke—228

- Minidonta simulata* Solem & Cooke—11  
*Minidonta extraria* Cooke & Solem—1  
 Station 103, second cave east of gap, Aukena Islet. D. Anderson. May 28, 1934.  
*Anceyodonta subconica* Solem & Cooke—1  
*Anceyodonta sexlamellata* (Pfeiffer)—4  
*Anceyodonta obesa* Solem—6  
*Anceyodonta hamyana* (Ancey)—3  
*Gambiodonta grandis* Cooke & Solem—3  
*Gambiodonta pilsbryi aukenensis* Cooke & Solem—1  
 Station 104, north side of Aukena Islet. D. Anderson. May 28, 1934.  
*Anceyodonta sexlamellata* (Pfeiffer)—1  
 Station 105, damp flat area near Ganhutu, Mangareva Islet, under stones. Y. Kondo. May 29, 1934.  
*Anceyodonta obesa* Solem—4  
 Station 107, flat area at 3 to 5 ft. elevation, in wave cutting, Akamaru Islet. D. Anderson and C. M. Cooke, Jr. May 30, 1934.  
*Anceyodonta sexlamellata* (Pfeiffer)—190  
*Anceyodonta hamyana* (Ancey)—2  
 Station 123, flat area, 200 ft. inland, on open ground along trail through village, Taravai Islet. D. Anderson. June 1, 1934.  
*Anceyodonta hamyana* (Ancey)—2  
 Station 126, in sand sweepings, Taravai Islet. D. Anderson. June 1, 1934.  
*Anceyodonta sexlamellata* (Pfeiffer)—13  
*Anceyodonta hamyana* (Ancey)—2  
*Anceyodonta densicostata* Cooke & Solem—1  
*Minidonta extraria* Cooke & Solem—1  
 Station 139, flat area 5 to 200 ft. inland, at 3 to 25 ft. elevation,

valley near Ganhutu, Mangareva Islet, under stones and on dead leaves. Y. Kondo and C. M. Cooke, Jr. June 3, 1934.

*Anceyadanta sexlamellata* (Pfeiffer)—1

*Anceyadanta ganhutuensis* Cooke & Solem—1

*Anceyadanta sarar* Solem—2

Station 142, flat area 150 ft. inland, at 6 ft. elevation, Ganhutu, Mangareva Islet. Y. Kondo and C. M. Cooke, Jr. June 3, 1934.

*Anceyadanta sorar* Solem—3

*Anceyadanta andersani* Cooke & Solem—9

*Anceyadanta abesa* Solem—10

*Anceyadanta hamyana* (Ancey)—13

*Anceyadanta difficilis* Solem—3

*Anceyadanta densicostata* Cooke & Solem—1

*Gambiadanta tumida* Cooke & Solem—23

*Gambiadanta pilsbryi pilsbryi* Cooke & Solem—26

*Gambiadanta mirabilis* Cooke & Solem—7

Station 155, gardens of Rikitea at 5 ft. elevation, Mangareva Islet. Y. Kondo and C. M. Cooke, Jr. June 4, 1934.

*Anceyadanta sexlamellata* (Pfeiffer)—1

*Anceyadanta sorar* Solem—1

*Anceyadanta abesa* Solem—4

*Anceyadanta hamyana* (Ancey)—2

*Gambiadonta mangarevana* Solem & Cooke—3

Station 156, flat area 3 to 10 ft. inland, at 2 ft. elevation, Rikitea, Mangareva Islet, under dead *hala* leaves. Lyons, Enas, and Y. Kanda. June 4, 1934.

*Anceyadanta abesa* Solem—1

Station 187, north part of Rikitea, at 6 ft. elevation, Mangareva Islet. Y. Kondo. June 7, 1934.

*Rikitea insalens* Solem—1

*Anceyadanta ganhutuensis* Cooke & Solem—1

*Anceyadanta sexlamellata* (Pfeiffer)—15

*Anceyadanta andersani* Cooke & Solem—2

*Anceyadanta difficilis* Solem—6

*Anceyadanta abesa* Solem—9

*Anceyadanta hamyana* (Ancey)—6

*Anceyadanta subconica* Solem & Cooke—1

*Gambiadanta mangarevana* Solem & Cooke—1

*Minidanta simulata* Solem & Cooke—1

Station 189, flat area, 6 ft. inland, at 2 ft. elevation, north end of Rikitea, Mangareva Islet. Y. Kanda and C. M. Cooke, Jr. June 8, 1934.

*Anceyadanta subcanica* Solem & Cooke—1

*Anceyadanta sarar* Solem—3

*Anceyadanta difficilis* Solem—13

*Anceyadanta sexlamellata* (Pfeiffer)—15

*Anceyadanta andersani* Cooke & Solem—3

*Anceyadanta difficilis* Solem—13

*Anceyadanta abesa* Solem—22

*Anceyadanta hamyana* (Ancey)—8

*Gambiadanta mangarevana* Solem & Cooke—2

Station 195, 100 feet inland, hillside back of beach, northwest side of Agakauitai Islet, on sandy soil. D. Anderson. June 8, 1934.

*Anceyadanta subcanica* Solem & Cooke—2

*Anceyadanta sexlamellata* (Pfeiffer)—47

*Anceyadanta hamyana* (Ancey)—8

*Anceyadanta abesa* Solem—4

*Gambiadanta agakauitaiana* Solem & Cooke—17

*Gambiadonta grandis* Cooke & Solem—32

*Minidonta simulata* Solem & Cooke—1

Station 197, 2 to 6 ft. inland, at 1 to 3 ft. elevation, northeast of Vaituatai Bay, Mangareva Islet. D. Anderson and C. M. Cooke, Jr. June 9, 1934.

*Anceyadanta sexlamellata* (Pfeiffer)—5

*Anceyadanta andersoni* Cooke & Solem—2

*Anceyadanta abesa* Solem—6

*Anceyadanta hamyana* (Ancey)—6

*Gambiadanta tumida* Cooke & Solem—9

*Gambiadanta mirabilis* Cooke & Solem—2

*Minidanta extraria* Cooke & Solem—1

Station 277, 100 to 200 yd. inland, Ganhutu, northeast end of Mangareva Islet, on open ground. D. Anderson. June 26, 1934.

*Anceyadanta ganhutuensis* Cooke & Solem—3

*Anceyadanta subcanica* Solem & Cooke—6

*Anceyadanta sarar* Solem—9

*Anceyadanta sexlamellata* (Pfeiffer)—7

*Anceyadanta andersani* Cooke & Solem—9

*Anceyadanta densicostata* Cooke & Solem—28

*Anceyadanta abesa* Solem—51

*Anceyadanta hamyana* (Ancey)—31

*Anceyadanta difficilis* Solem—3

*Gambiadanta tumida* Cooke & Solem—1

*Gambiadanta pilsbryi pilsbryi* Cooke & Solem—62

*Gambiadanta mirabilis* Cooke & Solem—28

### Rapa Island

Because of the extraordinary diversity and extensive anatomical data available for the endodontid taxa from Rapa Island, basic information on collecting history and intergeneric relationships were presented in Solem (1976b, pp. 490–492). Reference should be made to that report before proceeding further. All of the taxa could be derived from an *Opanara*-like ancestor.

The collecting localities from which endodontids were taken are shown in Figure 114. The discontinuity in numbering represents stations from ecologically disturbed or destroyed areas, stations where only arboreal or freshwater taxa were obtained, or a few stations from which fewer than a dozen specimens of land snails were obtained. In conversations with Yoshio Kondo and Elwood Zimmerman, estimates were given that in 1934 at least 70% of the area on Rapa Island had the native vegetation completely removed through a combination of agriculture, burning, depredations of goats, rats, and introduced plants. J. F. Gates Clarke (1971, p. 9) reported that in the late 1960s the forest areas had shrunk significantly since 1934.

It is thus obvious that the available sampling of the endemic land snail fauna found on Rapa came from less than 30% of the actual land area. Thus, in subsequent discussions of diversity, although the area of Rapa is given as 14.2 square miles, the actual area available for sampling was significantly less. Using data in the catalogue and collections of the Bishop Museum, including data as published in Baker (1938, 1940, 1941), Cooke & Kondo (1960), Kondo (1962), Solem (1976b), and a rough survey of other taxa, a conservative treatment of the land snail fauna of Rapa is summarized in Table LXIX. The presence of 100 land snail species, only two of which are introduced, makes this one of the, if not the, outstanding example of land snail diversity known to date. Efforts by Harald Rehder to collect endodontids on Rapa in recent years failed, and I suspect that much of this incredible radiation is extinct. As was discussed previously, many of the classic phenomena of speciation can be traced as taking place or having taken place on Rapa (Solem, 1976b, p. 491). Mountain-top relicts, a generalized high altitude form showing moderate subspeciation with derived lowland species, and intraspecific geographic structural variations, were all represented. These patterns leave no doubt in my mind that an island the size of Rapa was more than large enough to permit allopatric speciation to occur. This, of course, contrasts greatly with the statement of Diamond (1977) that in the



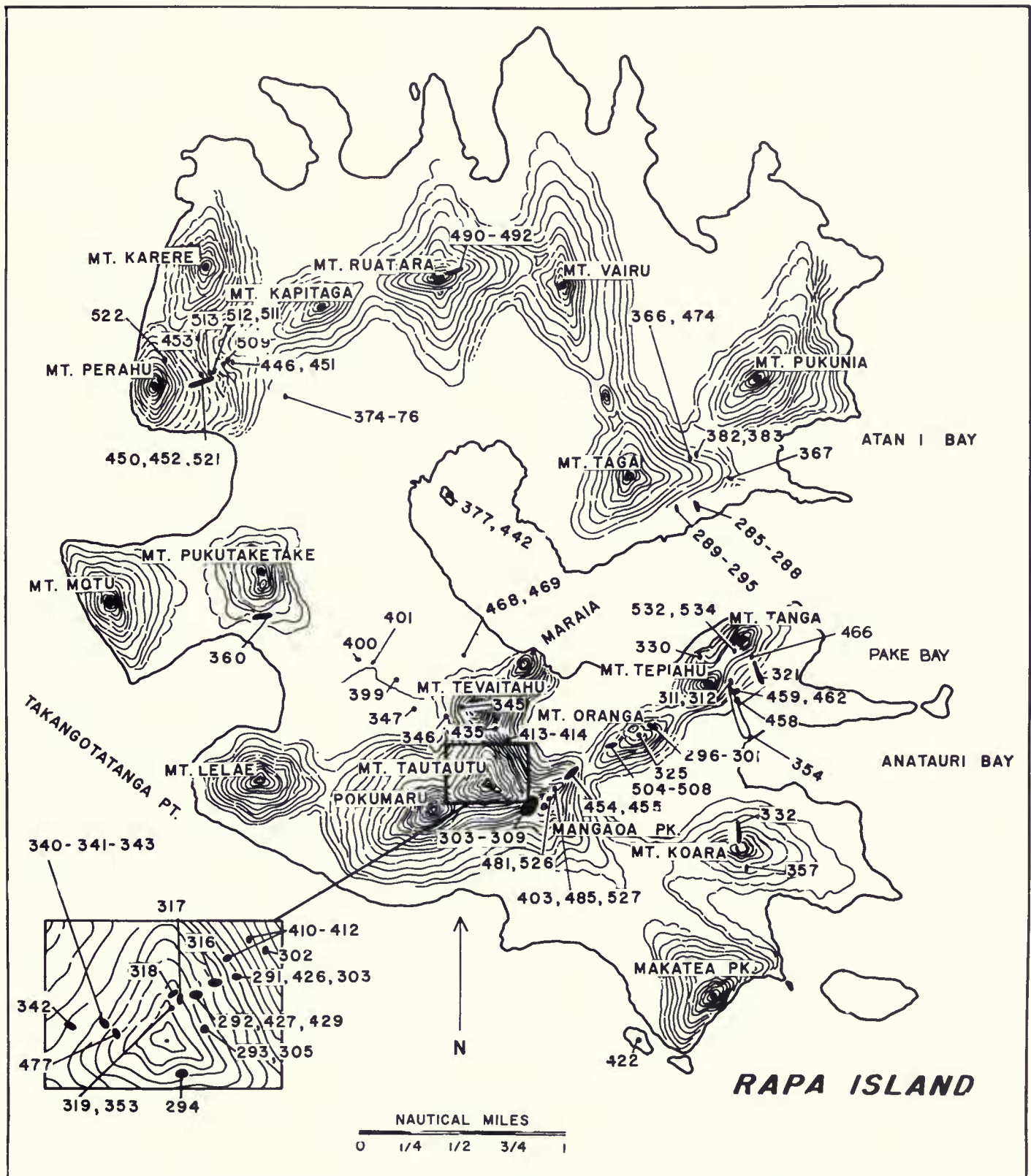


FIG. 114. Collecting localities on Rapa Island, Austral Islands. Mangarevan Expedition, 1934. Stations from which no endodontids were collected are omitted. The label for Station 466, just north of Station 321 and south of Mt. Tanga, was accidentally omitted.

Pacific no islands except New Guinea and possibly New Zealand were large enough for speciation in birds to occur and the questioning of White (1978, pp. 248-249) as to whether sympatric speciation would have been necessary on Rapa among the cryptorhynchine weevils on Rapa as revised by Zimmerman (1938).

Although many of the collecting localities on Rapa were restricted to extremely small geographic areas, in other sections a single station might have extended over several hundred vertical feet of cliff crawling. Thus the data are not strictly comparable in terms of area sampled or collecting effort. For example, the last

TABLE LXIX. - LAND SNAIL FAUNA OF  
RAPA ISLAND

Prosobranchs	15
Tornatellinidae	45
Pupillidae	6
Partulidae	1
Endodontidae	24
Helicarionidae	7
Subulinids	2
TOTAL	100

station made on Rapa Island, Station 534, produced 548 specimens of one species, representing an obvious effort to make "one last killing." Nevertheless, full data on local abundance is presented here. The map in Figure 114 is copied directly from the original station map at the B. P. Bishop Museum, which in turn is based on a pre-1900 French chart that was recognized as being somewhat inaccurate. Nevertheless, it will provide the best possible guide for any attempts to re-collect these areas. Because a number of the stations included apparent hybrids between two species of *Rhysoconcha*, presentation of the complete station list was deemed desirable.

#### The stations are:

Station 291A, hillside, ridge, valley and flat, Maitua region, back of Aurei, at 500 to 600 ft. elevation in coffee plantation under stones. Donald Anderson and C. M. Cooke, Jr. July 2, 1934.

Intergrades between *Rhysoconcha variumbilicata* and *R. atanuiensis*—32

*Ruataro oparica reductidentata* Solem—260

Station 292, damp hillside 100 yd. below base of cliff, Maitua region at 700 to 800 ft. elevation under stones. Donald Anderson and C. M. Cooke, Jr. July 2, 1934.

*Ruataro oparica reductidentata* Solem—14

Station 292, in native forest with some coffee trees, about 75 ft. higher than Station 291. Donald Anderson and C. M. Cooke, Jr. July 2, 1934.

*Ruataro oparica reductidentata* Solem—24

Station 293, damp hillside 100 yd. below base of cliff, Maitua at 700 to 800 ft. elevation under stones. Donald Anderson and C. M. Cooke, Jr. July 2, 1934.

*Ruataro oparica reductidentata* Solem—6

Station 296, hillside, SE valley of Orangi at 550 to 600 ft. elevation under stones and logs, on dead twigs, in rat-eaten kukui nuts, under *Polypodium* roots. Donald Anderson and C. M. Cooke, Jr. July 2, 1934.

*Rhysoconcha atanuiensis* Solem—13

Station 299, hillside above Station 296, SE valley, NE Orangi at 600 to 700 ft. elevation under stones and logs, on dead leaves. Donald Anderson and C. M. Cooke, Jr. July 3, 1934.

*Rhysoconcha atanuiensis* Solem—1

Station 302, lowest clump of coffee plantation on ridge, 100 yd. below Station 291, Maitua at 450 ft. elevation under stones. Donald Anderson and C. M. Cooke, Jr. July 4, 1934.

*Ruataro oparica reductidentata* Solem—1

Station 303, flat, in Maitua region at 500 ft. elevation under stones. (= Station 291). C. M. Cooke, Jr. July 4, 1934.

Intergrade between *Rhysoconcha variumbilicata* and *R. atanuiensis* Solem—1

Station 304, hillside, Maitua region under stones between Station 291 and Station 293. C. M. Cooke, Jr. July 4, 1934.

*Rhysoconcha variumbilicata* Solem—11

Station 305A, flat, hillside, valley, ridge, Maitua region, mostly under stones. Donald Anderson. July 4, 1934.

Intergrades between *Rhysoconcha variumbilicata* and *R. atanuiensis* Solem—15

*Ruataro oparica reductidentata* Solem—2

Station 305B, hillside, medium, in Maitua region, under stones (= Station 293). Donald Anderson. July 4, 1934.

*Rhysoconcha variumbilicata* Solem—7

Station 306, damp hillside, in Maitua region, between cliff and Station 305, under stones. Donald Anderson. July 4, 1934.

*Ruataro oparica reductidentata* Solem—1

Station 307, hillside, in Maitua region, under stones, or dead leaves. C. M. Cooke, Jr. July 4, 1934.

*Ruataro oparica reductidentata* Solem—1

Station 308, damp hillside in Maitua region at 800 ft. elevation, under stones, on cliffs and dead leaves. Donald Anderson, C. M. Cooke, Jr. July 4, 1934.

*Orangia maituatensis* Solem—6

Station 311, medium hillside Tepiahu region, at 800 to 850 ft. elevation. S. Wight and Y. Kondo. July 4, 1934.

*Orangia cookei cookei* Solem—4

Station 312, damp hillside, in Tepiahu region at 850 ft. elevation under stones. Donald Anderson. July 5, 1934.

*Orangia cookei cookei* Solem—67

Station 316, medium hillside, Maitua region at 500 to 750 ft. elevation, under stones and on dead leaves. C. M. Cooke, Jr. July 6, 1934.

*Opanara areaensis areaensis* Solem—4

*Ruataro oparica reductidentata* Solem—5

Station 316, in Maitua region, about ¼ m. E of Station 292, from first large coffee patch to near base of cliff. C. M. Cooke, Jr. July 6, 1934.

*Ruataro oparica reductidentata* Solem—1

Station 317, damp hillside, Maitua region at 750 ft. elevation under stones and on dead leaves. C. M. Cooke, Jr. July 6, 1934.

*Opanara areaensis areaensis* Solem—2

*Ruataro oparica reductidentata* Solem—10

*Orangia maituatensis* Solem—14

Station 318, damp hillside back of Maitua, E side, at 700 ft. elevation, under stones in moist woods. Donald Anderson. July 6, 1934.

*Rhysoconcha atanuiensis* Solem—10

*Ruataro oparica reductidentata* Solem—8

Station 319, damp hillside near *marae* back of Maitua, at 750 ft. elevation, under stones. Donald Anderson. July 6, 1934.

Intergrades between *Rhysoconcha variumbilicata* and *R. atanuiensis*—2

*Opanara areaensis areaensis* Solem—1

Station 321, hillside, Pake Bay, from bottom to top of ridge. Y. Kondo. July 6, 1934.

*Rhysoconcha atanuiensis* Solem—1

*Orangia cookei cookei* Solem—39

Station 325, hillside, medium, South side Orangi, at 850 ft. elevation under stones. Raymond Fosberg. July 6, 1934.

*Orangia cookei cookei* Solem—15

Station 330, damp hillside, NW of Tepiahu, ridge, at 500 to 650 ft. elevation, under stones in forest with coffee predominating. Donald Anderson. July 7, 1934.

*Rhysoconcha atanuiensis* Solem—4

Station 333, in damp forest, SW of Anatauri Bay, just above Station 332, at 650 to 700 ft. elevation, under stones. Donald Anderson. July 7, 1934.

*Orangia sporadica* Solem—2

Station 340, damp flat NW of Mt. Tautautu, at 600 to 700 ft. elevation, mostly under stones, very few on dead leaves. C. M. Cooke, Jr. July 9, 1934.

*Opanara areaensis areaensis* Solem—83

*Orangia sporadica* Solem—24

Station 342, damp valley NW of Mt. Tautautu at 600 to 700 ft. elevation, under stones. Donald Anderson, C. M. Cooke, Jr. July 9, 1934.

*Rhysoconcha atanuiensis* Solem—4

*Ruataro oparica reductidentata* Solem—15



Station 346, damp hillside and valley, W of Tavaithahu, at 750 ft. elevation, under stones in forest. Donald Anderson. July 9, 1934.

*Rhysconcha atanuiensis* Solem—2

*Opanara areaensis areaensis* Solem—11

*Kondoconcha othnius* Solem—31

Station 347, hillside and valley forest patch, E slope of Mt. Tavaithahu, at 350 to 400 ft. elevation, under stones. Donald Anderson. July 9, 1934.

*Rhysconcha atanuiensis* Solem—8

Station 353, along side of *narac* just below Mangaoa, Maitua region, under wet stones in wet forest. Donald Anderson. July 10, 1934.

Intergrades between *Rhysconcha variumbilicata* and *R. atanuiensis* Solem—24

*Opanara areaensis areaensis* Solem—1

*Ruatara oparica reductidentata* Solem—5

Station 354, north side of Tepiahu, from sea to just below Station 311. Yoshio Kondo. July 10, 1934.

*Orangia cookei cookei* Solem—46

Station 357, medium hillside, Oromange, Mt. Koara, at 800 ft. elevation, in good forest, under stones. Harold St. John. July 11, 1934.

*Ruatara koarana* Solem—4

*Orangia sporadica* Solem—3

Station 358, Maitua region at 550 ft. elevation. All specimens under a single log. Raymond Fosberg. July 11, 1934.

Intergrades between *Rhysconcha variumbilicata* and *R. atanuiensis* Solem—7

Station 358, Maitua region. All specimens from under one log resting on *honohono*. Raymond Fosberg, July 11, 1934.

Intergrades between *Rhysconcha variumbilicata* and *R. atanuiensis* Solem—2

*Opanara areaensis areaensis* Solem—5

*Ruatara oparica reductidentata* Solem—29

Station 360, hillside, ridge, and valley, Morongoto, under dead fern fronds and stones. Donald Anderson and Elwood Zimmerman. July 12, 1934.

*Ruatara oparica normalis* Pfeiffer—25

*Orangia sporadica* Solem—1

*Kondoconcha othnius* Solem—2

Station 366, damp hillside, above Area, at 400 ft. elevation under stones. Donald Anderson. July 12, 1934.

*Opanara arcaensis arcaensis* Solem—32

Station 367, dry hillside, side of Atanui Bay, at 300 to 400 ft. elevation, under stones in coffee plantation. Donald Anderson. July 12, 1934.

*Rhysconcha atanuiensis* Solem—62

Station 376, dry ridge, S slope of Mt. Perahu, at 900 to 1,000 ft. elevation, on ground, under moss. Elwood Zimmerman. July 13, 1934.

*Ruatara oparica normalis* Solem—6

Station 382, medium hillside, Area region, at 250 to 300 ft. elevation, under stones. Y. Kondo, Donald Anderson, and C. M. Cooke, Jr. July 15, 1934.

*Opanara areaensis areaensis* Solem—31

Station 383, medium hillside, Area region, at 250 to 450 ft. elevation, under stones and on dead leaves. Y. Kondo, Donald Anderson, and C. M. Cooke, Jr. July 15, 1934.

*Rhysconcha atanuiensis* Solem—1

*Opanara areaensis areaensis* Solem—126

Station 399, ridge, Maraia region, at 500 ft. elevation, open ground on dead leaves. Donald Anderson, C. M. Cooke, Jr., and Yoshio Kondo. July 16, 1934.

*Ruatara oparica normalis* Solem—30

Station 400, near crest of main ridge, SW of Morongoto valley, at 800 ft. elevation. W. Anderson, Y. Kondo, and Donald Anderson. July 16, 1934.

*Ruatara oparica normalis* Solem—4

*Orangia sporadica* Solem—3

Station 401, 3rd small valley SW of Morongoto, about 100 ft. below crest of main ridge on W side of ridge. Capt. Anderson, C. M. Cooke, Jr., and Y. Kondo. July 16, 1934.

*Orangia sporadica* Solem—12

Station 403, hillside, W slope, NE ridge of Mt. Mangaoa, at 800 to

900 ft. elevation, under stones in small forest patch in small ravine. Donald Anderson. July 16, 1934.

*Rhysconcha variumbilicata* Solem—34

*Opanara areaensis areaensis* Solem—1

*Orangia sporadica* Solem—9

Station 414, Titikaveka valley N of Station 411, valley, at 500 ft. elevation, under stones and logs. Y. Kondo and C. M. Cooke, Jr. July 18, 1934.

*Rhysconcha atanuiensis* Solem—1

Station 426, damp hillside, Maitua region, 500 ft. elevation, in coffee plantation (= Station 291). Y. Kondo and C. M. Cooke, Jr. July 20, 1934.

Intergrades between *Rhysconcha variumbilicata* and *R. atanuiensis* Solem—48

*Ruatara oparica reductidentata* Solem—15

Station 427, Maitua region, under stones (= Station 292). Y. Kondo and C. M. Cooke, Jr. July 20, 1934.

*Rhysconcha variumbilicata* Solem—12

*Opanara megoniphala megoniphala* Solem—9

*Ruatara oparica reductidentata* Solem—8

Station 429, Maitua region at about 500 ft. elevation (= Station 292 and Station 294). Shells mixed. Yoshio Kondo. July 28, 1934.

*Ruatara oparica reductidentata*—5

*Orangia maituatensis*—1

Station 435, damp hillside, NE of Mt. Tautautu (E Maitua), near base of cliffs, under stones and on dead leaves. Donald Anderson. July 20, 1934.

*Rhysconcha atanuiensis* Solem—33

*Orangia sporadica* Solem—20

Station 442, damp hillside, Tupui Islet, at 20 ft. elevation, on dead kukui leaves and twigs. S. Wight and C. M. Cooke, Jr. July 21, 1934.

*Rhysconcha atanuiensis* Solem—1

Station 446, damp E ridge of Mt. Perahu at 1,200–1,500 ft. elevation, under stones and trash in forest. D. Anderson. July 21, 1934.

*Opanara areaensis microtorma* Solem—1

*Opanara bitridentata* Solem—2

*Opanara perahuensis* Solem—3

*Opanara duplicidentata* Solem—6

*Ruatara oparica normalis* Solem—1

*Orangia cookei montana* Solem—2

Station 450, damp upper part of E ridge, Mt. Perahu at 1,500 to 1,900 ft. elevation, on ground at base of bird's nest fern leaves. Raymond Fosberg. July 21, 1934.

*Opanara fosbergi* Solem—4

*Opanara bitridentata* Solem—41

*Opanara duplicidentata* Solem—2

Station 451, damp E ridge of Mt. Perahu, at 1,200 to 1,500 ft. elevation. Yoshio Kondo. July 21, 1934.

*Opanara duplicidentata* Solem—18

*Opanara depasoapicata* Solem—10

*Opanara areaensis microtorma* Solem—1

*Opanara bitridentata* Solem—5

*Ruatara oparica normalis* Solem—2

*Orangia sporadica* Solem—1

*Orangia cookei montana* Solem—16

Station 452, damp edge E of Mt. Perahu, flat, at 1,500 to 1,800 ft. elevation. Yoshio Kondo. July 21, 1934.

*Opanara duplicidentata* Solem—8

*Opanara depasoapicata* Solem—2

*Opanara areaensis microtorma* Solem—1

*Opanara perahuensis* Solem—1

*Ruatara oparica normalis* Solem—4

*Orangia sporadica* Solem—1

Station 453, E ridge of Mt. Perahu, at 1,800 to 1,900 ft. elevation. Yoshio Kondo. July 21, 1934.

*Rhysconcha atanuiensis* Solem—1

*Opanara caliculata* Solem—2

*Opanara bitridentata* Solem—3

*Opanara perahuensis* Solem—4

Station 454, halfway up Mt. Mitiperu, under stones and in dirt. D. Anderson. July 21, 1934.

*Ruatara oparica normalis* Solem—7

Station 455, two-thirds way up Mt. Mitiperu, from valley back of village, under stones. Capt. Anderson. July 21, 1934.

*Ruatara oparica normalis* Solem—18

Station 458, hillside S side of Mt. Tepiahu, at 500 ft. elevation. Y. Kondo and C. M. Cooke, Jr. July 23, 1934.

*Opanara negomphala tepiahuensis* Solem—37

Station 459, damp hillside, S side of Mt. Tepiahu at 550 ft. elevation, under stones and on dead leaves. C. M. Cooke, Jr. July 23, 1934.

*Opanara megomphala tepiahuensis* Solem—84

Station 462, damp hillside, S side of Mt. Tepiahu at 550 ft. elevation. Yoshio Kondo. July 23, 1934.

*Orangia cookei cookei* Solem—23

Station 466, hillside, S side of Mt. Tanga, at 700 to 800 ft. elevation, under stones and on dead leaves. D. Anderson. July 23, 1934.

*Ruatara oparica oparica* (Anton, 1839)—25

*Orangia cookei cookei* Solem—542

Stations 468-470, damp valley, Kopenena, at 200 to 600 ft. elevation. S. Wight and Y. Kondo. July 24, 1934.

*Ruatara oparica normalis* Solem—5

Station 474, damp hillside back of Area, at 400 ft. elevation, under stones. Donald Anderson. July 24, 1934.

*Rhysoconcha atanuiensis* Solem—5

*Opanara areaensis* Solem—440

Station 477, damp hillside NW of Mt. Tautautu, above Station 340, at 800 ft. elevation, under stones, logs, and dead leaves. S. Wight, Y. Kondo, and C. M. Cooke, Jr. July 25, 1934.

*Opanara areaensis densa* Solem—18

*Opanara negomphala megomphala* Solem—5

*Orangia maituatensis* Solem—1

Station 478, damp hillside, NW of Mt. Tautautu, at 750 ft. elevation, under stones. Yoshio Kondo. July 25, 1934.

*Opanara areaensis areaensis* Solem—13

*Opanara areaensis densa* Solem—1

*Orangia cookei tautautuensis* Solem—9

Station 479, N face of Mt. Tautautu, at 800 ft. elevation, under stones and logs. C. M. Cooke, Jr. July 25, 1934.

*Orangia sporadica* Solem—1

Station 481, damp ridge, NE Mangaoa Peak, at 1,000 to 1,200 ft. elevation, in and beneath litter under tree fern. Elwood Zimmerman. July 25, 1934.

*Opanara altiapica* Solem—1

Station 485, medium damp hillside, W slope, NE ridge of Mangaoa, at 800 ft. elevation, under stones. Donald Anderson. July 25, 1934.

*Rhysoconcha variumbilicata* Solem—56

*Rhysoconcha atanuiensis* Solem—10

*Opanara areaensis areaensis* Solem—29

*Orangia sporadica* Solem—6

Station 490, hillside, NE slope Mt. Ruatara, at 750 ft. elevation. Yoshio Kondo. July 26, 1934.

*Ruatara oparica normalis* Solem—67

Station 491, Mt. Ruatara, higher than Station 490, at 800 ft. elevation. Yoshio Kondo. July 26, 1934.

*Ruatara oparica normalis* Solem—201

Station 491, damp hillside, NE slope of Mt. Ruatara, flat at 800 ft. elevation. Yoshio Kondo. July 26, 1934.

*Ruatara oparica normalis* Solem—179

Station 492, hillside, NE slope of Mt. Ruatara, flat at 900 ft. elevation. Yoshio Kondo. July 26, 1934.

*Ruatara oparica normalis* Solem—1

Station 504, above cemetery, Ahurei. Capt. Donald Anderson. July 28, 1934.

*Rhysoconcha atanuiensis* Solem—1

Station 509, E ridge of Mt. Perahu, at 1,300 to 1,550 ft. elevation, under stones, logs, and dead leaves. Yoshio Kondo, D. Anderson, and natives. July 28, 1934.

*Opanara fosbergi* Solem—1

*Opanara depasoapicata* Solem—3

*Opanara areaensis microtorma* Solem—2

*Opanara perahuensis* Solem—4

*Opanara duplicitata* Solem—2

*Ruatara oparica normalis* Solem—1

*Orangia cookei montana* Solem—21

Station 511, E ridge of Mt. Perahu, at 1,600 to 1,800 ft. elevation, on *Freycinetia*, ferns, and shrubs. Yoshio Kondo, D. Anderson, and natives. July 28, 1934.

*Opanara duplicitata* Solem—1

Station 512, E end, main ridge of Mt. Perahu, at 1,500 to 1,850 ft. elevation, under moss and between leaves of birds' nest ferns. Donald Anderson and natives. July 28, 1934.

*Rhysoconcha atanuiensis* Solem—2

*Opanara caliculata* Solem—6

*Opanara bitridentata* Solem—28

*Opanara duplicitata* Solem—1

*Ruatara oparica normalis* Solem—2

Station 513, E end, main ridge of Mt. Perahu, at 1,600 to 1,800 ft. elevation, on logs and dead leaves. Yoshio Kondo. July 28, 1934.

*Opanara bitridentata* Solem—2

*Opanara duplicitata* Solem—1

*Ruatara oparica normalis* Solem—10

*Orangia sporadica* Solem—2

Station 521, E ridge Mt. Perahu, at 1,500 to 1,800 ft. elevation. Elwood Zimmerman. July 28, 1934.

*Orangia cookei montana* Solem—1

Station 526, NE ridge, Mt. Mangaoa, at 1,000 to 1,100 ft. elevation, under dead leaves. Elwood Zimmerman and Donald Anderson. July 29, 1934.

*Rhysoconcha atanuiensis* Solem—1

*Opanara altiapica* Solem—23

*Ruatara oparica normalis* Solem—10

Station 527, hillside, in small ravine, NE ridge of Mt. Mangaoa, at 800 ft. elevation, mostly under stones, some in trash of birds' nest fern. Elwood Zimmerman and Donald Anderson. July 29, 1934.

*Rhysoconcha variumbilicata* Solem—9

*Rhysoconcha atanuiensis* Solem—1

*Opanara areaensis areaensis* Solem—11

*Ruatara oparica normalis* Solem—20

*Orangia sporadica* Solem—17

Station 532, medium damp hillside, N side of Mt. Tanga S of bay, at 300 to 700 ft. elevation, under stones. Toto, Terii Pare, and Donald Anderson. July 31, 1934.

*Orangia cookei cookei* Solem—1

Station 534, hillside, S Mt. Tanga, E of Teutu, under stones. Toto, Terii Pare, and Donald Anderson. July 31, 1934.

*Orangia cookei cookei* Solem—548

In partial summary of the data on joint species occurrences, 10 stations had three species of endodontids, usually each belonging to a different genus (Stations 317, 346, 333, 360, 403, 427, and 526). At Stations 477 and 478, two species of *Opanara* occurred with another genus, and at Station 450 only three species of *Opanara* were found. Stations 453, 485, and 513 had four endodontids with either two or three species of *Opanara*; Stations 512 and 527 had five species each with two or three *Opanara*; Stations 446 and 452 had six species, each with four *Opanara*; and Stations 451 and 509 had seven species, the former with four and the latter with five species of *Opanara*. Most of the stations with high diversity represent segments of the Mt. Perahu climb and range over 200 to 400 vertical feet. Thus, the degree of "same rock" sympatry is untested, but since several of the *Opanara* species have been collected from 1,200 to 1,900 ft. on Mt. Perahu and the species show distinct character displacement and species recognition features of the terminal genitalia, they are assumed to have been microsympatric. The concentration of taxa on Mt. Perahu may be an artifact of partial extinction because this highly inaccessible peak would have been one of the last areas to



be decimated by goats, rats, ants, and the vegetative vermin of human introduction.

The concentration of sympatry in *Opanara* is in part because it was the most speciose genus on Rapa and probably in part because it was the most generalized and thus presumably nearest the colonizing stock.

All of the Rapan endodontids could have evolved from a single colonization.

### Austral Islands

Except for the taxa named by Pfeiffer (1846a) and Garrett (1879), all available material dated from the Mangarevan Expedition of 1934. Unfortunately, at most of the stations, only dead specimens were obtained, although frequently in rather large quantities. A few specimens of *Punctum* were found on Tubuai and Raivavae, whereas *Discocharopa aperta* was taken in limited quantities on Rurutu. By far, the predominant members of the fauna are *Australdonta*, which is endemic, and the few species of *Minidonta*. There is a distinct morphologic gap between the two genera, with differences being far more striking than those between *Minidonta* and *Anceyodonta* on Mangareva. Nevertheless, it is quite probable that *Australdonta* represents a local derivative from *Minidonta*.

Although stations were not directly plotted for Rurutu (fig. 115), the map is published to show the approximate geographic features used to locate the stations. Information on relative abundance is given only for those stations at which two or more species were collected. On Rurutu, a maximum of five species was taken at Station 760, with four species found at Station 748. On Tubuai (fig. 116) the diversity is markedly lower, with only three *Australdonta* and one *Punctum* taken. At three stations there were two species collected. Raivavae (fig. 117) had four *Minidonta* and two *Australdonta* collected at Station 652, but otherwise only one to three species per station. In none of these situations were there clear indications of species exclusion.

On Rimatara, only the endemic *Australdonta rimatarana* Solem, 1976, and an extremely abundant colony, possibly introduced, of *Australdonta degagei* (Garrett, 1879) were found. The 1,552 specimens of the latter represent the single largest sample of an endodontid available to me.

*Punctum*, *Minidonta*, and *Discocharopa* clearly are independent colonizations, whereas *Australdonta* is a locally evolved genus, probably from *Minidonta*.

#### RURUTU (Fig. 115)

Station 748, hillside, ¼ mile inland at 250 ft. elevation, N of village, Mato Naa, dead shells at foot of cliff. Y. Kondo and C. M. Cooke, Jr. August 25, 1934.

*Minidonta haplaenopla* Solem—69

*Australdonta degagei* (Garrett)—11

*Australdonta yoshii* Solem—115

*Australdonta magnasulcata* Solem—1

Station 754, hillside, ⅓ mile inland at 200 ft. elevation, Mato Naa,

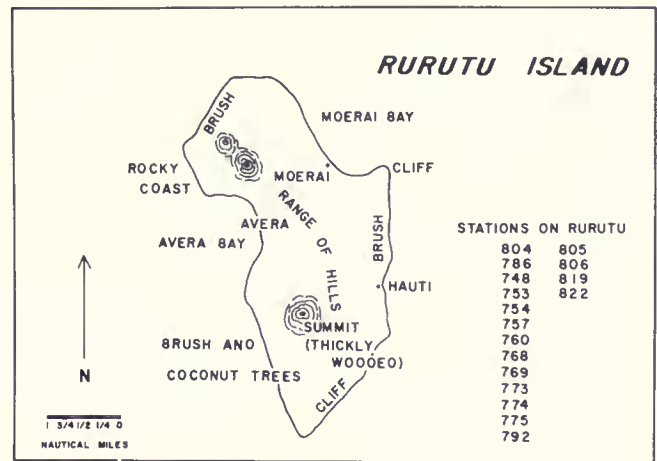


FIG. 115. Major geographic features on Rurutu, Austral Islands.

near foot of cliff under ironwood trash. C. M. Cooke, Jr. August 25, 1934.

*Australdonta pseudplanulata* Solem—1

*Australdonta degagei* (Garrett)—52

Station 760, 20 to 30 yd. inland, at 5 to 15 ft. elevation, bluff N of Moerai, Mato Naa, dry, under stones, on cliffs and dead leaves. Y. Kondo and C. M. Cooke, Jr. August 26, 1934.

*Discocharopa aperta* (Möllendorff)—6

*Australdonta pseudplanulata* Solem—8

*Australdonta degagei* (Garrett)—3

*Australdonta tapina* Solem—19

*Australdonta magnasulcata* Solem—3

Station 769, cave above Station 769, bluff S of Moerai, low makatea cliff, SE of Moerai, Mato Arei, flat, dry, under stones. D. Anderson. August 26, 1934.

*Australdonta degagei* (Garrett)—42

*Australdonta tapina* Solem—5

Station 775, high makatea cliff SE of Moerai at 50 to 150 ft. elevation, under stones and logs. Y. Kondo and D. Anderson. August 27, 1934.

*Discocharopa aperta* (Möllendorff)—6

*Australdonta degagei* (Garrett)—31

*Australdonta tapina* Solem—2

Station 786, N side of bluff N of Hauti at 40 to 75 ft. elevation, on ground under trash. Harold St. John. August 28, 1934.

*Australdonta pseudplanulata* Solem—35

*Australdonta degagei* (Garrett)—1

Station 792, S side of cliff at 10 to 50 ft. elevation, Mato Naa, under stones and logs, on dead leaves. D. Anderson. August 29, 1934.

*Minidonta haplaenopla* Solem—7

*Australdonta degagei* (Garrett)—13

Station 804, N of Averai, sweepings. Y. Kondo, D. Anderson, and C. M. Cooke, Jr. August 31, 1934.

*Australdonta tapina* Solem—32

*Australdonta degagei* (Garrett)—4

Station 805, 50 to 100 ft. inland at 5 to 30 ft. elevation, makatea cliff, N of Averai. Y. Kondo and D. Anderson. August 31, 1934.

*Australdonta pseudplanulata* Solem—3

*Australdonta degagei* (Garrett)—19

*Australdonta tapina* Solem—18

Station 819 (=815), mouth of shallow cave, on hillside at 50 ft. elevation, Mato Arapia. Y. Kondo and C. M. Cooke, Jr. September 2, 1934.

*Australdonta tapina* Solem—17

*Australdonta magnasulcata* Solem—1

#### TUBUAI (Fig. 116)

Station 698, 300 to 400 yd. inland, SW of Murivai, under *Barringtonia* trees. Y. Kondo and D. Anderson. August 16, 1934.

*Punctum polynesianum* Solem—2

*Australdonta tubuaiana* Solem—6

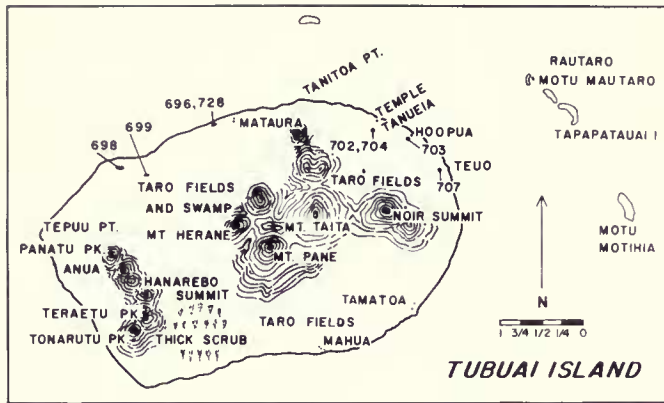


FIG. 116. Collecting localities on Tubuai, Austral Islands. Mangarevan Expedition, 1934.

Station 699, S of Murivai at 6 to 8 ft. elevation, dead specimens in sandy soil on trail. Y. Kondo and D. Anderson. August 16, 1934.

*Australdonta radiella radiella* (Pfeiffer)—136

*Australdonta tubuaiana* Solem—11

Station 703, 200 to 300 yd. inland at 5 ft. elevation, S of Hoopua, in sandy soil. Y. Kondo and D. Anderson. August 18, 1934.

*Australdonta radiella radiella* (Pfeiffer)—81

*Australdonta pharcata* Solem—2

#### RAIVAVAE (Fig. 117)

Station 622, ½ mile W of Ahuovi Point, 10 to 30 ft. inland at 5 ft. elevation, on dead leaves. Y. Kondo, D. Anderson, and C. M. Cooke, Jr. August 9, 1934.

*Punctum polynesianum* Solem—1

*Minidonta gravacosta* Solem—39

*Australdonta raivavaeana* Solem—3

Station 633, hillside at 50 to 150 ft. elevation, ¼ mile E of Anatonu village. Y. Kondo and C. M. Cooke, Jr. August 10, 1934.

*Minidonta anatonuana* Solem—2

*Minidonta planulata* Solem—3

*Australdonta raivavaeana* Solem—18

Station 636, hillside at 150 to 500 ft. elevation, ¼ mile E of Anatonu village. Y. Kondo and C. M. Cooke, Jr. August 10, 1934.

*Minidonta anatonuana* Solem—2

*Australdonta raivavaeana* Solem—3

Station 652, hillside at 50 to 150 ft. elevation, ¼ mile E of Anatonu village. Y. Kondo and D. Anderson. August 11, 1934.

*Minidonta micraconica* Solem—4

*Minidonta anatonuana* Solem—29

*Minidonta sulcata* Solem—4

*Minidonta planulata* Solem—4

*Australdonta raivavaeana* Solem—68

*Australdonta ectopia* Solem—5

#### Society Islands

Unfortunately, the fabled Society Islands were not investigated adequately for land snails in the early 1800s because most visitors had other interests. As summarized by Solem (1976b, pp. 385-386), there were five distinct periods of collecting that produced examples of *Libera*. Most of those taxa taken prior to 1900 were not found in 1934 by members of the Mangarevan Expedition, who did not collect any *Libera* below 4,000 ft. elevation. One specimen of *Mautodontha* was taken possibly as low as 3,500 ft. in 1934 (Station 860), whereas examples of the charopid genus *Sinployea* were found practically at seashore level in both the

1930s and 1970s. Evidence from other studies (for example Solem, 1972b) indicates that the early collectors did not work the mountain peaks. I am thus concluding that the material collected pre-1900 and not found subsequently represented lowland taxa that have become extinct in the past century. The monumental work of Garrett (1884) indicated geographic differences in lowland species distributions on both Moorea and Tahiti, but modern confirmation of this proved impossible during 1974 and 1977 collecting trips.

There is at least moderate sympatry of taxa on Mt. Aorai (Stations 862-870), where malacologists did the collecting and provided adequate samples. A maximum of six species was found at Station 865. On Mt. Orofena and above Papenoo, where the botanists Fosberg and St. John made similar transects, two species were found only at Station 949, probably indicating less skilled collecting efforts. On Moorea, modern (since 1920) collecting has yielded only *Sinployea modicella*. On Huahine, two species were taken at Station 1008, whereas on Tahaa and Borabora two to four species were taken per station. Comments on species differences in the sympatric *Libera* were given by Solem (1976b), and the data are not repeated here.

Although the total diversity of endodontoid land snails in the Society Islands was great, little information can be deduced concerning species interactions because of extinctions and lack of anatomical material for most groups. The endodontids were collected in lowland areas as late as 1880, but by 1934 were restricted to zones above 3,500 ft. elevation and may be extinct today. The Charopidae still exist at low population levels on several islands.

*Sinployea*, *Discocharopa*, and *Mautodontha* represent independent arrivals, with *Nesodiscus* and *Libera* local derivatives from *Mautodontha*.

#### TAHITI

Station 862, Mt. Aorai, small ravine west of ridge at 4,600 ft. elevation. Kondo and Anderson. September 13, 1934.

*Sinployea tahitiensis* Solem—6

*Mautodontha zimmermani* Solem—1

Station 863, Mt. Aorai, top of ridge between 2nd and 3rd camps at 4,700 to 5,500 ft. elevation. Zimmerman, Kondo, and D. Anderson. September 14, 1934.

*Sinployea tahitiensis* Solem—4

*Mautodontha zimmermani* Solem—1

*Libera bursatella bursatella* (Gould)—169

*Libera cookeana* Solem—1

Station 864, Mt. Aorai, 5,500 to 5,600 ft. elevation. Zimmerman, Kondo, and D. Anderson. September 15, 1934.

*Mautodontha zimmermani* Solem—1

*Libera bursatella bursatella* (Gould)—35

*Libera cookeana* Solem—2

Station 865, Mt. Aorai, trail near ridge at 5,600 to 6,300 ft. elevation. Zimmerman, Kondo, Anderson. September 15, 1934.

*Sinployea tahitiensis* Solem—2

*Punctum* sp.—1

*Mautodontha zimmermani* Solem—5

*Libera bursatella bursatella* (Gould)—62

*Libera cookeana* Solem—3

*Libera micrasoma* Solem—13



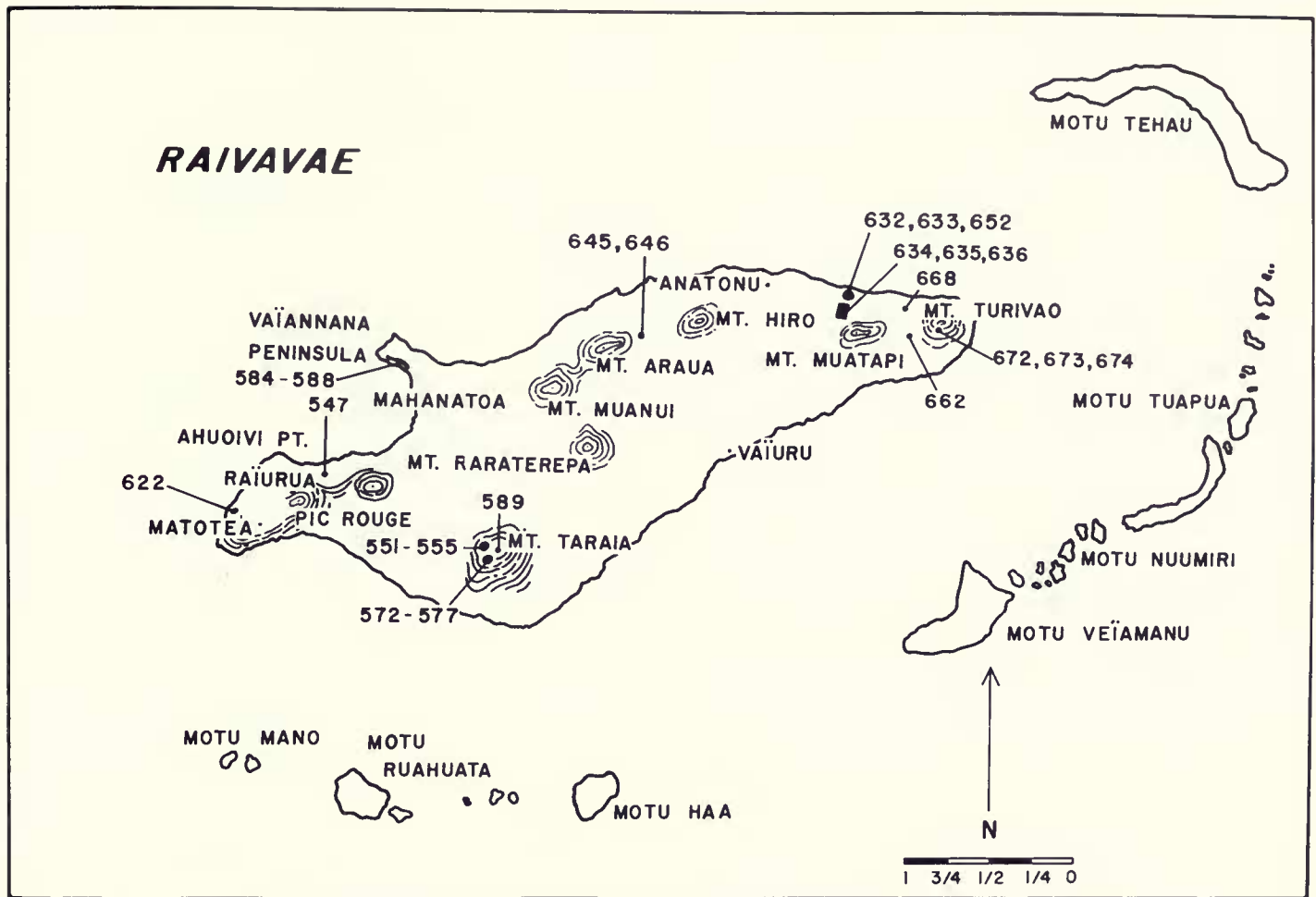


FIG. 117. Collecting localities on Raivavae, Austral Islands. Mangarevan Expedition, 1934.

Station 866, Aorai Mt., valley west of trail at 6,000 ft. elevation. Zimmerman, Kondo, and Anderson. September 15, 1934.

*Sinployea montana* Solem—3  
*Libera bursatella bursatella* (Gould)—90  
*Libera micrasoma* Solem—6

Station 867, Aorai Mt., 4,700 to 6,300 ft. elevation. Zimmerman, Kondo, and Anderson. September 16, 1934.

*Sinployea tahitiensis* Solem—8  
*Mautodontha zimmermani* Solem—2  
*Libera bursatella bursatella* (Gould)—11

Station 869, Aorai Mt., 5,000 ft. elevation. Zimmerman and Kondo. September 16, 1934.

*Libera bursatella bursatella* (Gould)—1  
*Mautodontha zimmermani* Solem—1

Station 870, Aorai Mt., valley west of trail at 5,000 ft. elevation. D. Anderson. September 16, 1934.

*Mautodontha (M.) aoraiensis* Solem—2  
*Sinployea lamellicosta* (Garrett)—12  
*Libera bursatella bursatella* (Gould)—9

Station 949, Mt. Orofena, east end of south ridge at 4,500 ft. elevation. R. Fosberg and H. St. John. September 20, 1934.

*Libera bursatella orofenensis* Solem—18  
*Libera umbilicata* Solem—4

#### HUAHINE

Station 1008, Tiva, 100 yd. inland at 6 ft. elevation, on dead leaves. Anderson and Kondo. October 3, 1934.

*Nesodiscus huaheinensis* (Pfeiffer)—1  
*Sinployea neglecta* Solem—81

#### TAHAA

Station 1081, east ridge of Mt. Purauti at 1,200 to 1,400 ft. elevation. Gessler, Kondo, and Anderson. October 11, 1934.

*Nesodiscus fabrefactus* (Pease)—7  
*Nesodiscus fictus* (Pease)—719

Station 1085, valley southeast of Mt. Purauti at 800 ft. elevation. Zimmerman. October 11, 1934.

*Nesodiscus fabrefactus* (Pease)—3  
*Nesodiscus fictus* (Pease)—265

#### BORABORA

Station 1091, south slope of Pahio-Temanu ridge at 800 ft. elevation. Gessler and St. John. October 13, 1934.

*Nesodiscus tanae* (Garrett)—1  
*Nesodiscus magnificus* Solem—1

Station 1093, south slope of Pahio-Temanu ridge, sweepings from entrance to cave under cliff at 800 ft. elevation. Gessler and St. John. October 13, 1934.

*Sinployea* sp.—1  
*Discocharopa aperta* (Möllendorff)—1  
*Mautodontha saintjohni* Solem—23  
*Nesodiscus tanae* (Garrett)—45

#### Cook Islands

Extensive collections, particularly on Rarotonga by Andrew Garrett, were made in the 1860s to early 1880s. The results were summarized in a faunistic sur-

vey (Garrett, 1881) that revealed one of the most striking endodontoid faunas found. Some additional collecting on the outer islands of the Cook Group was done by Peter Buck of the Bishop Museum in the 1920s. In 1964 and 1965, Laurie Price made significant collections on Rarotonga for Field Museum.

Garrett's collections showed that there had been a radiation of 10 species of *Sinployea* on Rarotonga, of which only one, plus an 11th species, could be obtained in the 1960s. Two of the three *Libera* described by Garrett have not been collected in this century, nor have the two species of *Mautodontha* described from Rarotonga been collected again. Price reached the top of the highest mountain peak on Rarotonga, collecting there a new subfamily of Tornatellinidae, *Tekoulina* (Solem, 1972b). The experiences of the Bishop Museum Mangarevan Expedition members on Tahiti in 1934 also resulted in obtaining many new taxa from higher elevations. These experiences indicate rather conclusively that Garrett restricted his collecting efforts to lower altitudes.

Garrett did publish some notes on joint occurrences of species, but no quantitative data. The collections made by Price on Rarotonga in 1964 and 1965 (fig. 118) were from most areas of the island, yet almost

none of Garrett's endodontoid species could be relocated. He obtained no sympatric occurrences of endodontoid species.

### Samoa

For the purposes of this discussion, both Western Samoa and American Samoa are considered to be a geographic unit. The early visits of the U.S. Exploring Expedition did not result in the description of any endodontoids, but the activities of the German trader Graeffe, representative of the Hamburg firm Goddefroy, resulted in the description of *Thaumatodon hystrielloides* (Mousson, 1865) and *Sinployea complementaria* (Mousson, 1865) plus some misidentified material and *Graeffedon graeffei* referred to in a later publication (Mousson, 1869). Description of *Sinployea allecta allecta* (Cox, 1870), based on material obtained by John Brazier, completed the early work prior to the collecting and summary provided by Garrett (1887b). Only scattered additional material was obtained prior to 1965 when Solem and Price collected extensively on Upolu (fig. 119) and Savai'i (fig. 120).

The endodontoid fauna of Samoa is more diverse at a generic than a specific level. There is a modest radiation of *Sinployea* into six species-level taxa, but other-

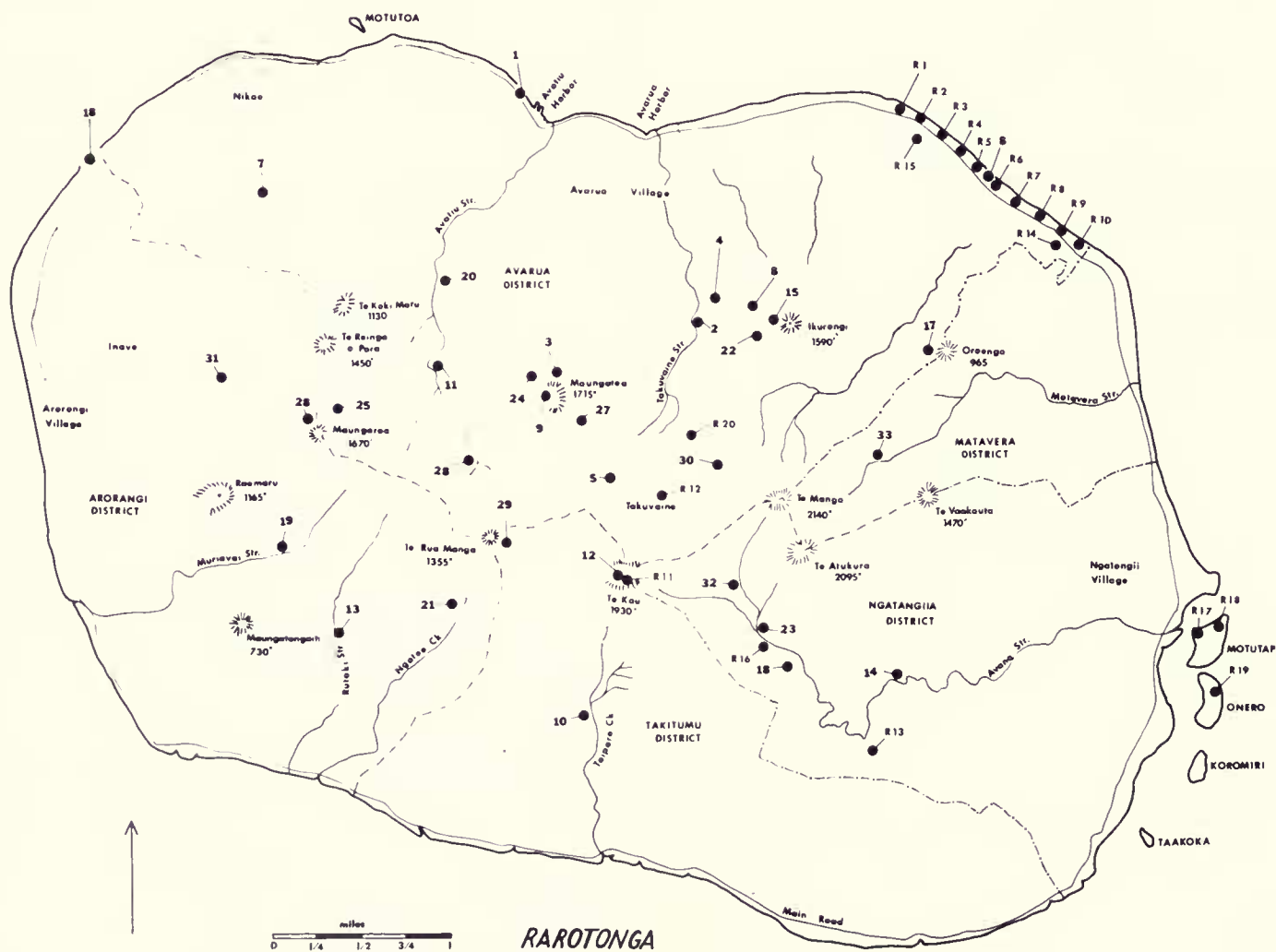


FIG. 118. Collecting localities on Rarotonga, Cook Islands. L. Price, 1964 and 1965.



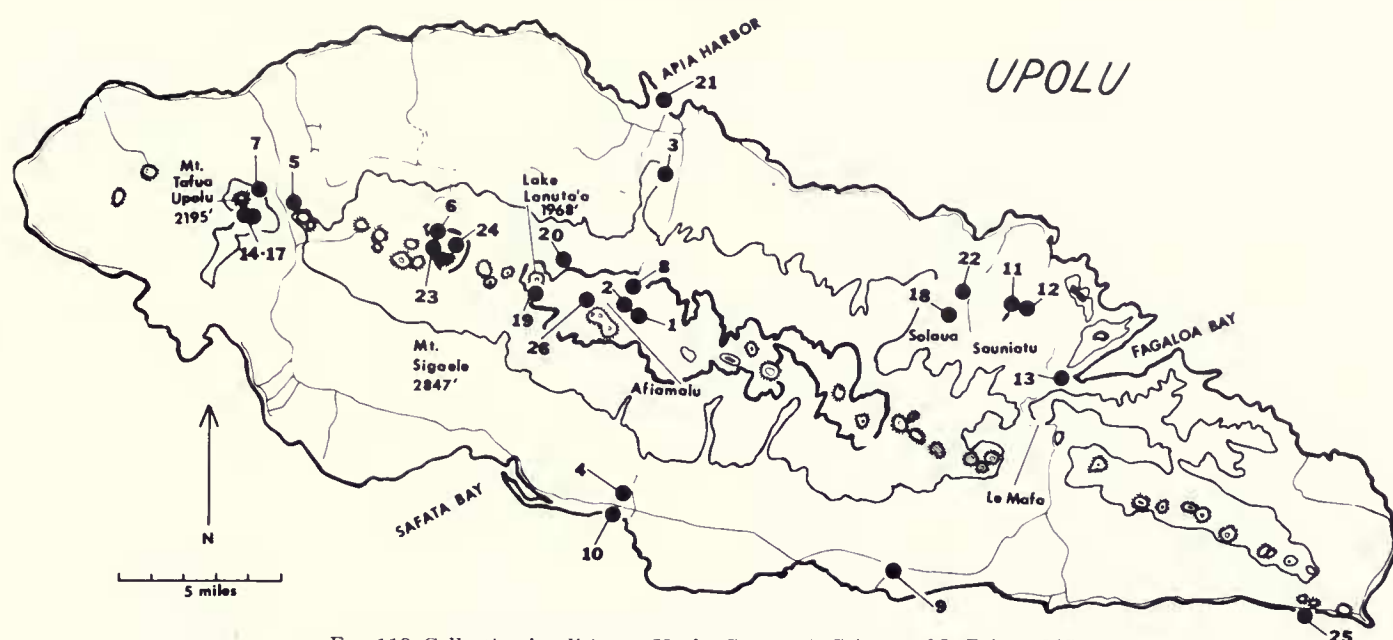


FIG. 119. Collecting localities on Upolu, Samoa. A. Solem and L. Price, 1965.

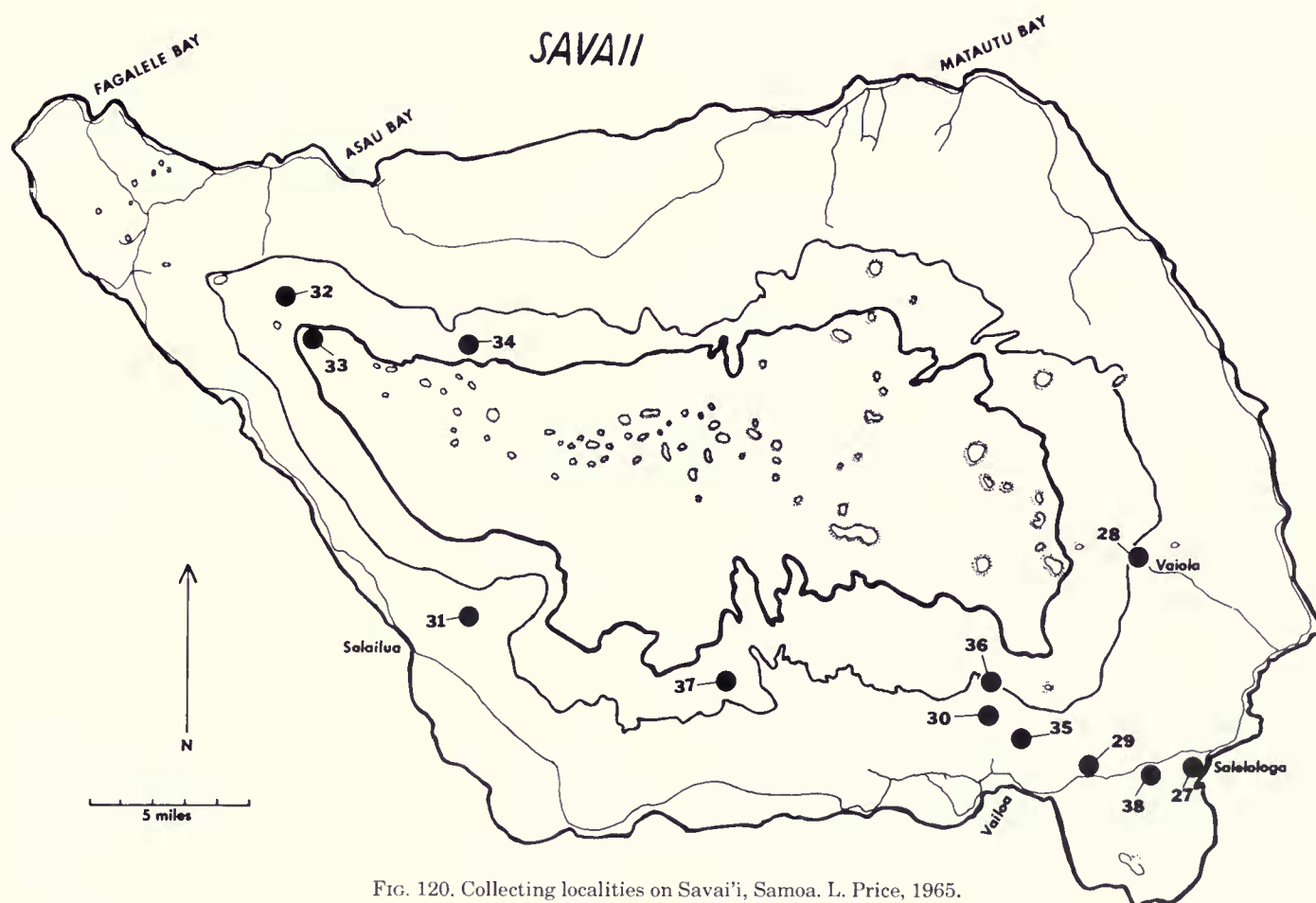


FIG. 120. Collecting localities on Savai'i, Samoa. L. Price, 1965.

wise there are only *Minidonta manuaensis* from the Manua Group, scattered records for *Discocharopa aperta* (Möllendorff, 1888), *Thaumatodon hystricelloides* (Mousson, 1865) from Upolu, *Graeffedon graeffei* from Upolu, and *G. savaiiensis* from Savai'i. The distributional peculiarities of *Sinployea* have been discussed above (pp. 82–83). On Ta'u, all known

material was obtained from litter sweepings as dead specimens, with *Minidonta manuaensis*, *Discocharopa aperta*, *Sinployea clausa*, *S. aunuuana*, and *S. allecta tauensis* recorded. Their actual degree of sympatry is unknown. From Olosega only the first two species are known. The two taxa reported from Savai'i were taken at separate stations, and only on Upolu is there any

indication of sympatry. At Station 7, there were one *Sinployea clista* and three *S. a. allecta*; Station 18 had two *S. clista* and 59 *S. complementaria*; Station 19 had 18 *S. complementaria* and 90 *Thaumatodon hystricelloides*; Station 24 had three *S. complementaria* and five *T. hystricelloides*; and Station 39 had 18 *S. complementaria* and one *Graeffedon graeffei*. At all other stations on Upolu, only one species was obtained.

One indication of change is the fact that *Thaumatodon hystricelloides* was, in the 1870s, "not uncommon under rotten wood and beneath decaying leaves," behind Apia (Garrett, 1887b, p. 131), whereas in the mid-1960s it was restricted to elevations above 1,800 ft., probably because of predation by introduced ants. *Graeffedon* is only known from scattered individuals and apparently always was quite rare. Except for occasional pockets of abundance, the various *Sinployea* species also were relatively uncommon.

Since none of the genera found in Samoa have close relationship, the fauna has resulted from multiple invasions. Except for *Sinployea* and *Graeffedon*, this has not been followed by speciation. One of the surprising results of my fieldwork in Samoa was determining that, almost without exception, the land snails of Upolu did not show any geographic speciation patterns despite the relatively large size of the island.

### Tonga

Surprisingly little material has been collected in Tonga. The early collections of Graeffe were reported on by Mousson (1871), and a few casual collections were made by staff members from the Bishop Museum in this century. Collections made in 1966 by Laurie Price added significant quantities of formerly known species and some new material.

The only records from the Ha'apai Group remain those given by Mousson (1871), despite the great number of islands present (fig. 121). Most information and collecting has resulted from work on Vava'u (fig. 122), Tongatapu (fig. 123), and Eua (fig. 124).

The degree of diversity on a generic level is relatively high, with *Thaumatodon* represented by two species, *T. euaensis* from Eua and *T. vavauensis* from Vava'u; the endemic genus *Tuimalila* represented by *T. pilsbryi* from Eua and *T. infundibulus* (Hombron & Jacquinot, 1841) from Vava'u; *Sinployea vicaria* (Mousson, 1871) has a wide distribution throughout the group, and a subspecies, *S. v. paucicosta*, is found on one portion of Vava'u; *Vatusila tongensis* lives on Eua; and *Graeffedon pricei* is known from Tongatapu. In all probability, each genus represents an independent colonization of Tonga.

The limited evidence available shows a moderate degree of sympatry. On Eua Island, at Station T-22, *Thaumatodon euaensis* (50), *Vatusila tongensis* (1), and *Tuimalila pilsbryi* (35) were obtained. On Vava'u, Station T-8 produced *Thaumatodon vavauensis* (7) and *Sinployea vicaria paucicosta* (16); Station T-9 had *S. v. paucicosta* (70) and *T. infundibulus* (2); Station T-10

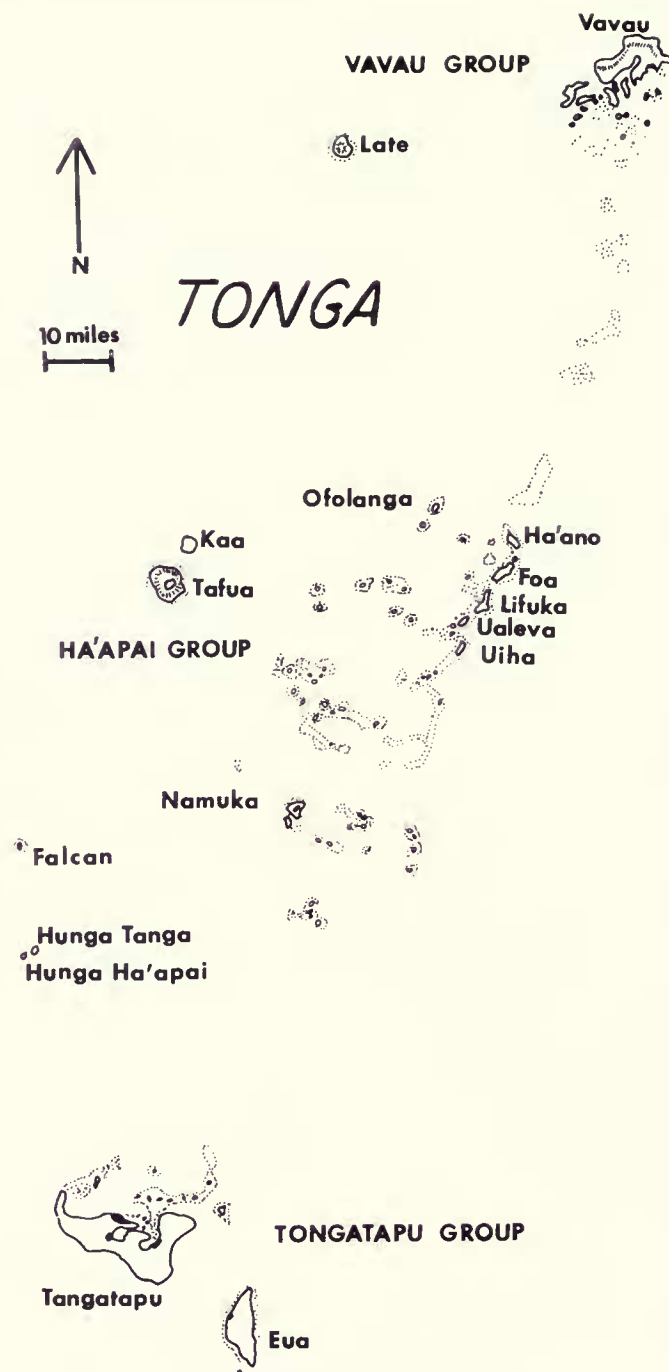


FIG. 121. Main islands of Tonga.

had *S. v. paucicosta* (3) and *T. infundibulus* (19); Station T-12 had one specimen of each species. On Tongatapu single specimens of *Graeffedon pricei* and *S. v. vicaria* were taken at Station T-4. These data do suggest fairly extensive sympatry among the Tongan genera.

### Lau Archipelago

The Lau Archipelago (fig. 125) is the one center of evolution for both the Endodontidae and Charopidae in which it is still possible to study species ecology and distribution with fair certainty of success. At present, only a small portion of the islands have been sampled adequately, and undoubtedly many additional taxa



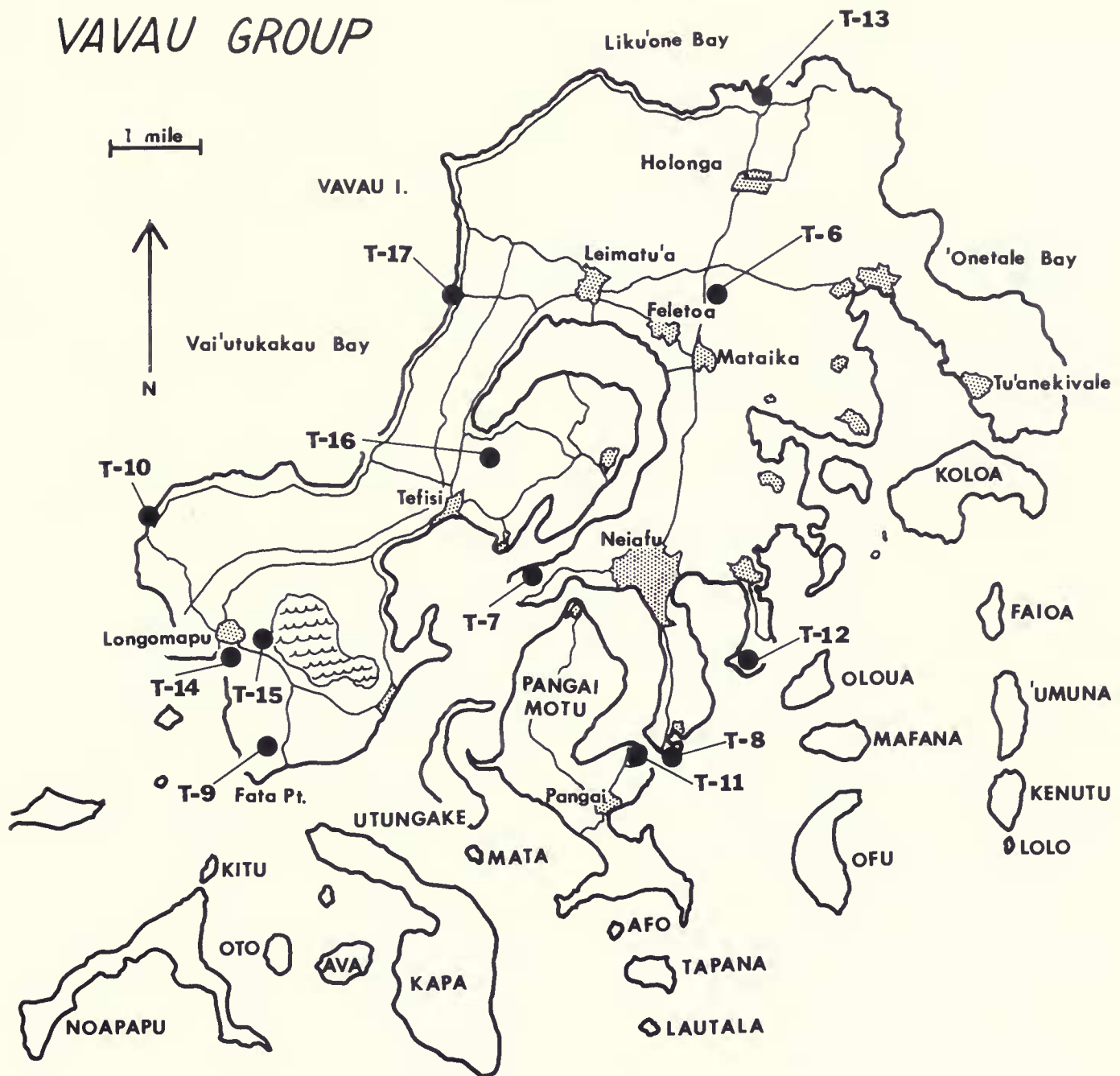


FIG. 122. Collecting localities on Vava'u, Tonga. L. Price, 1966.

will be found. The early description of *Sinployea inermis*, *S. adposita*, and *Thaumatodon subdaedalea* (Mousson, 1870) only hinted at the actual diversity. Solem (1973d, 1976b) described the endemic genera *Priceconcha* and *Zyzyxdonta* plus several *Thaumatodon*, and in this report an additional six species of *Sinployea*, two species of *Vatusila*, and the endemic genera *Maafu* and *Lauopa* are named. Collections made by L. Price in 1970 and by Walter Cernohorsky in 1977 (Solem, 1978a), confirm that taxa of both families are still extant.

Of the endodontids, *Thaumatodon* has a wide extralimital distribution, with *Priceconcha* and *Zyzyxdonta* representing locally evolved derivatives. Of the

charopids, *Vatusila*, *Discocharopa*, and *Sinployea* have wide extralimital ranges, but *Maafu* and *Lauopa* represent probable locally evolved taxa, and *Microcharopa* is shared only with Viti Levu.

The degree of sympatry is rather extensive, as shown by the following summary of Bishop Museum field collections:

Station 30, *Yangasa Levu*, south end of island, 150 ft. inland on hillside at 40 ft. elevation. H. S. Ladd. July 26, 1934.

*Sinployea inermis meridionalis* Solem—97

*Sinployea adposita* (Mousson)—67

*Sinployea lauensis* Solem—23

*Microcharopa mimula* Solem—2

*Discocharopa aperta* (Möllerndorff)—17

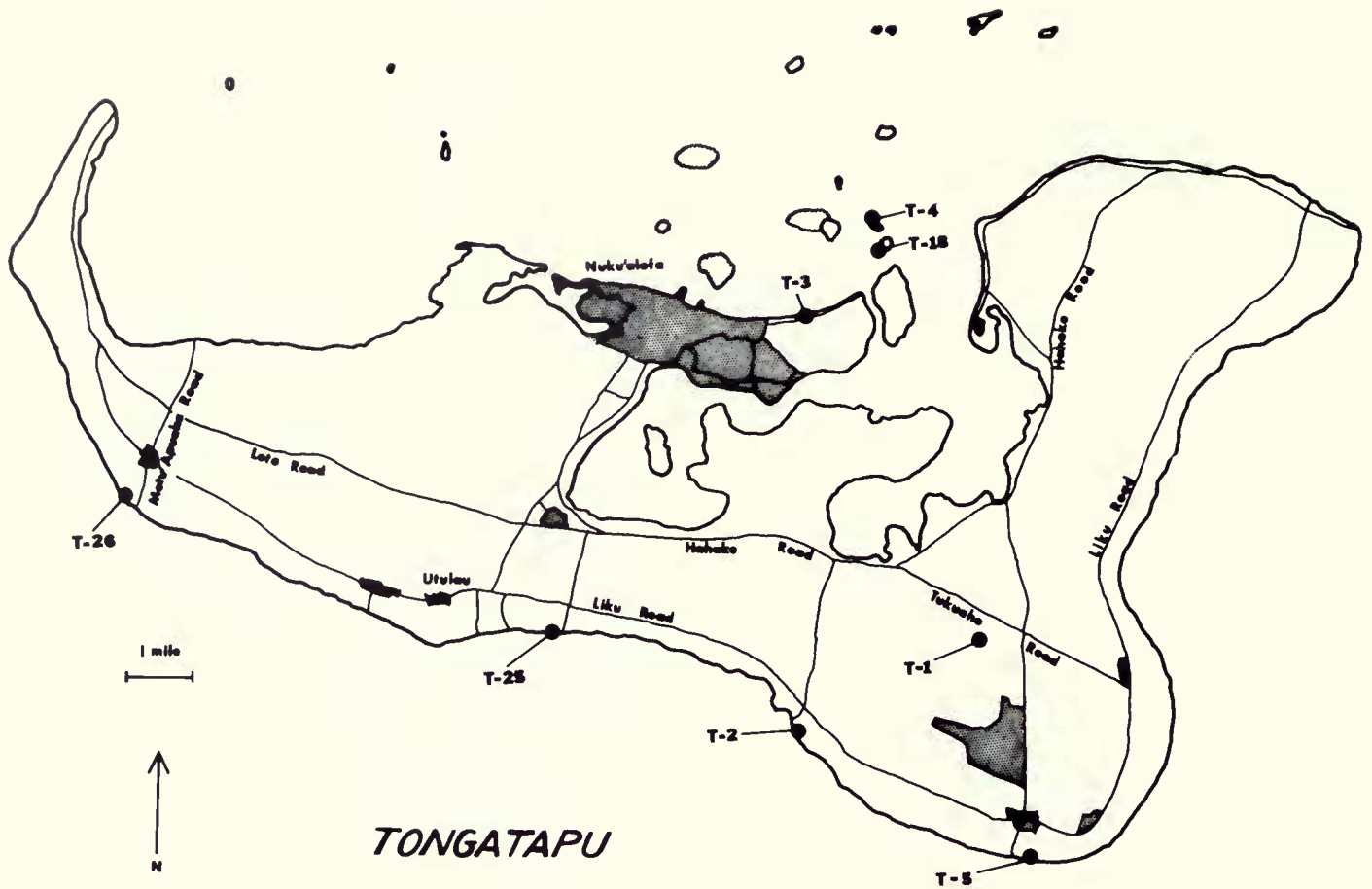


FIG. 123. Collecting localities on Tongatapu, Tonga. L. Price, 1966.

Station 28, *Navutu-i-Loma*, northeast  $\frac{1}{4}$  of island, limestone ridge 150 yd. inland at 100 ft. elevation. H. S. Ladd. July 24, 1934.

*Sinployea inermis meridionalis* Solem—2

*Sinployea lauensis* Solem—13

*Sinployea navutuensis* Solem—15

*Discocharopa aperta* (Möllerndorff)—3

*Zyzyxdonta alata* Solem—5

Station 29, *Navutu-i-Loma*, limestone ridge at 100 ft. elevation, 150 yd. inland. H. S. Ladd. July 24, 1934.

*Sinployea inermis meridionalis* Solem—50

*Sinployea lauensis* Solem—19

*Sinployea navutuensis* Solem—13

*Discocharopa aperta* (Möllerndorff)—1

*Zyzyxdonta alata* Solem—2

Station 2, *Namuka*, 500 ft. inland at 65 to 75 ft. elevation, north central point of island, Matandolo. H. S. Ladd. July 7, 1934.

*Sinployea angularis* Solem—109

*Microcharopa mimula* Solem—2

*Discocharopa aperta* (Möllerndorff)—6

Station 3, *Namuka*, 65 to 75 ft. elevation, 500 ft. inland, north central part of island, Matandolo, between rocks. H. S. Ladd. July 7, 1934.

*Sinployea angularis* Solem—79

*Discocharopa aperta* (Möllerndorff)—1

Station 27, *Wangava*, in soil and between rocks,  $\frac{1}{4}$  mile inland at 75 ft. elevation, northeast end of island. H. S. Ladd. July 22, 1934.

*Sinployea lauensis* Solem—6

*Sinployea recursa* Solem—108

*Discocharopa aperta* (Möllerndorff)—7

*Thaumatodon laddi* Solem—18

*Microcharopa mimula* Solem—4

*Karoni*, slope of peak at 90 ft. elevation under dry leaves. E. H. Bryan, Jr. August 15, 1924.

*Sinployea adposita* (Mousson)—9

*Discocharopa aperta* (Möllerndorff)—6

Station 40, *Aiwa*, 50 yd. inland at 25 ft. elevation, southwest  $\frac{1}{4}$  of island, Vataniyambia. H. S. Ladd. August 7, 1934.

*Sinployea inermis meridionalis* Solem—20

*Sinployea adposita* (Mousson)—7

*Discocharopa aperta* (Möllerndorff)—1

Station 97, *Lakemba*,  $\frac{1}{4}$  mile inland at 15 ft. elevation, from west end of *Toumba* to  $\frac{2}{5}$  mile distant. Zimmerman and Kondo. August 20, 1938.

*Sinployea inermis lakembana* Solem—10

*Sinployea adposita* (Mousson)—26

Station 43, *Nayau*,  $\frac{1}{2}$  mile inland at 250 ft. elevation, base of limestone cliff, Nauko. H. S. Ladd. August 13, 1934.

*Sinployea adposita* (Mousson)—4

*Sinployea lauensis* Solem—20

*Mafu thaumasius* Solem—65

*Discocharopa aperta* (Möllerndorff)—3

*Vatusila nayauana* Solem—42

*Microcharopa mimula* Solem—4

Station 101, *Nayau*, 100 yd. inland at 30 to 500 ft. elevation,  $\frac{3}{4}$  mile north of Liku village. Kondo. August 22, 1938.

*Sinployea adposita* (Mousson)—14

*Vatusila kondoi* Solem—56

Station 89, *Mango*,  $\frac{1}{2}$  to  $\frac{3}{4}$  mile south-southwest from Marona at 350–400 ft. elevation. Kondo. August 14, 1938.

*Sinployea inermis inermis* (Mousson)—13

*Thaumatodon corrugata* Solem—3

Station 90, *Mango*,  $\frac{1}{2}$  to  $\frac{3}{4}$  mile south-southwest from Marona at 200 to 300 ft. elevation. Kondo. August 14, 1938.

*Sinployea inermis inermis* (Mousson)—2

*Thaumatodon corrugata* Solem—1

Station 65, *Munia*,  $\frac{1}{2}$  mile inland at 600 to 900 ft. elevation, back of Hysik's home, northeast middle. Kondo. August 4, 1938.

*Sinployea adposita* (Mousson)—5

*Microcharopa mimula* Solem—2



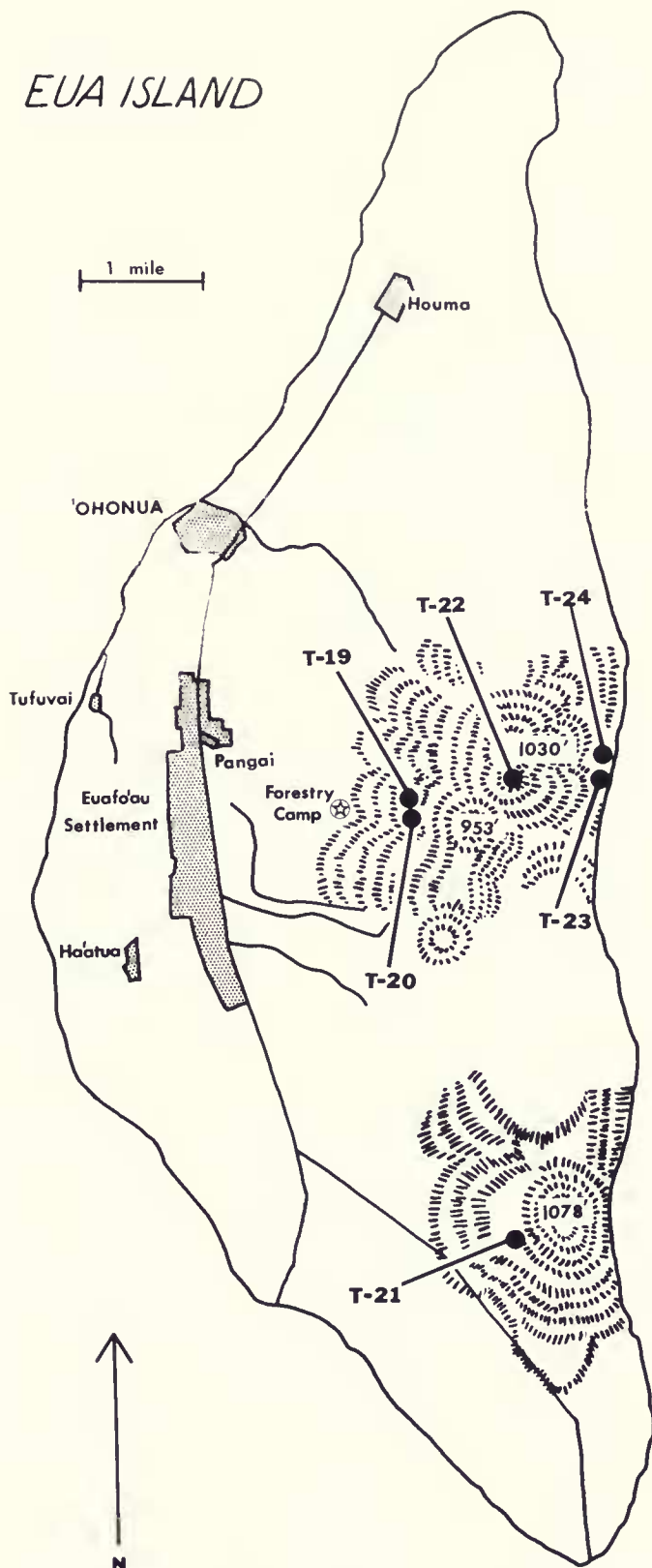


FIG. 124. Collecting localities on Eua, Tonga. L. Price, 1966.

Station 78, Vanua Mbalavu,  $\frac{3}{4}$  mile inland at 200 to 250 ft. elevation, limestone hill, between Valika and Mosomo Bay. Zimmerman and Kondo. August 9, 1938.

*Sinployea inermis inermis* (Mousson)—3  
*Lauopa mbalavuana* Solem—2  
*Discocharopa aperta* (Möllendorff)—4

### Fiji, Main Islands

Except for the description and record of *Sinployea princei* (Liardet, 1876) from Taveuni and Kandavu, all known endodontoids are from Viti Levu. Only charopids are recorded, with *Microcharopa*, *Lagivala*, *Discocharopa*, and *Sinployea* representing independent colonizations. The endemic genus *Ba* is a local derivative from *Sinployea*, which has only two species represented. There is no apparent pattern of geographic replacement or clear isolation to any part of Viti Levu for any species. Nowhere on Viti Levu are the taxa abundant. The very few instances of microsympatry are summarized in the following list of the Bishop Museum localities. In addition, I collected four examples of *Sinployea irregularis* (Garrett, 1887) with one specimen of *Ba humbugi* under a single log in 1965.

Station 151, Nangava Id., south coast near Suva. Yoshio Kondo. September 20, 1938.

*Sinployea godeffroyana* Solem—1  
*Lagivala minusculus* Solem—1

Station 47, Lami Ridge at 5 to 150 ft. elevation, 5 miles west of Suva. Kondo and C. M. Cooke. July 24, 1938.

*Microcharopa mimula* Solem—2  
*Lagivala vivus* Solem—1  
*Discocharopa aperta* (Möllendorff)—2

Near Sigatoka, base of limestone cliff,  $\frac{1}{2}$  to  $1\frac{1}{2}$  miles from shore. H. S. Ladd. July 12, 1928.

*Microcharopa mimula* Solem—1  
*Discocharopa aperta* (Möllendorff)—1

Station 122, northwest of Nangaranambulata Mt., 10 miles inland at 2,700 to 3,200 ft. elevation. Kondo. September 5, 1938.

*Sinployea irregularis* (Garrett)—1  
*Ba humbugi* Solem—1

Station 60, summit of Mt. Korobamba, 2 miles inland at 1,000 to 1,300 ft. elevation. Kondo, Jacob, and Zimmerman. August 1, 1938.

*Sinployea irregularis* (Garrett)—2  
*Ba humbugi* Solem—2

Station 133, 14 miles inland at 2,300 to 2,500 ft. elevation, at and above stream, 2 miles east of Vatuthere, Nandarivatu. Kondo. September 9, 1938.

*Sinployea godeffroyana* Solem—1  
*Sinployea irregularis* (Garrett)—31

### Ellice Islands

Despite their scattered nature and small size, a modest variety of endodontoids reached the Ellice Group. *Thaumatodon decemplicata* (Mousson, 1873) is known from Nukufetau and Vaitupu; *Sinployea pseudovicaria* from Vaitupu; *S. ellicensis* has subspecies on Funafuti and Nukulaelae; *Vatusila vaitupuensis* is known from Vaitupu; and the Pleistocene fossil *Lagivala davidi* (Ladd, 1968) has been recorded from Funafuti. Thus, at least four separate colonizations were involved.

The available data are such that I have no evidence as to possible sympatry among taxa recorded from the same island.

### Marshall Islands

The deep-core drillings on Bikini and Eniwetok resulted in finding Miocene to Pleistocene fossils belonging to *Vatusila*, *Cookeconcha*, and *Minidonta*. No

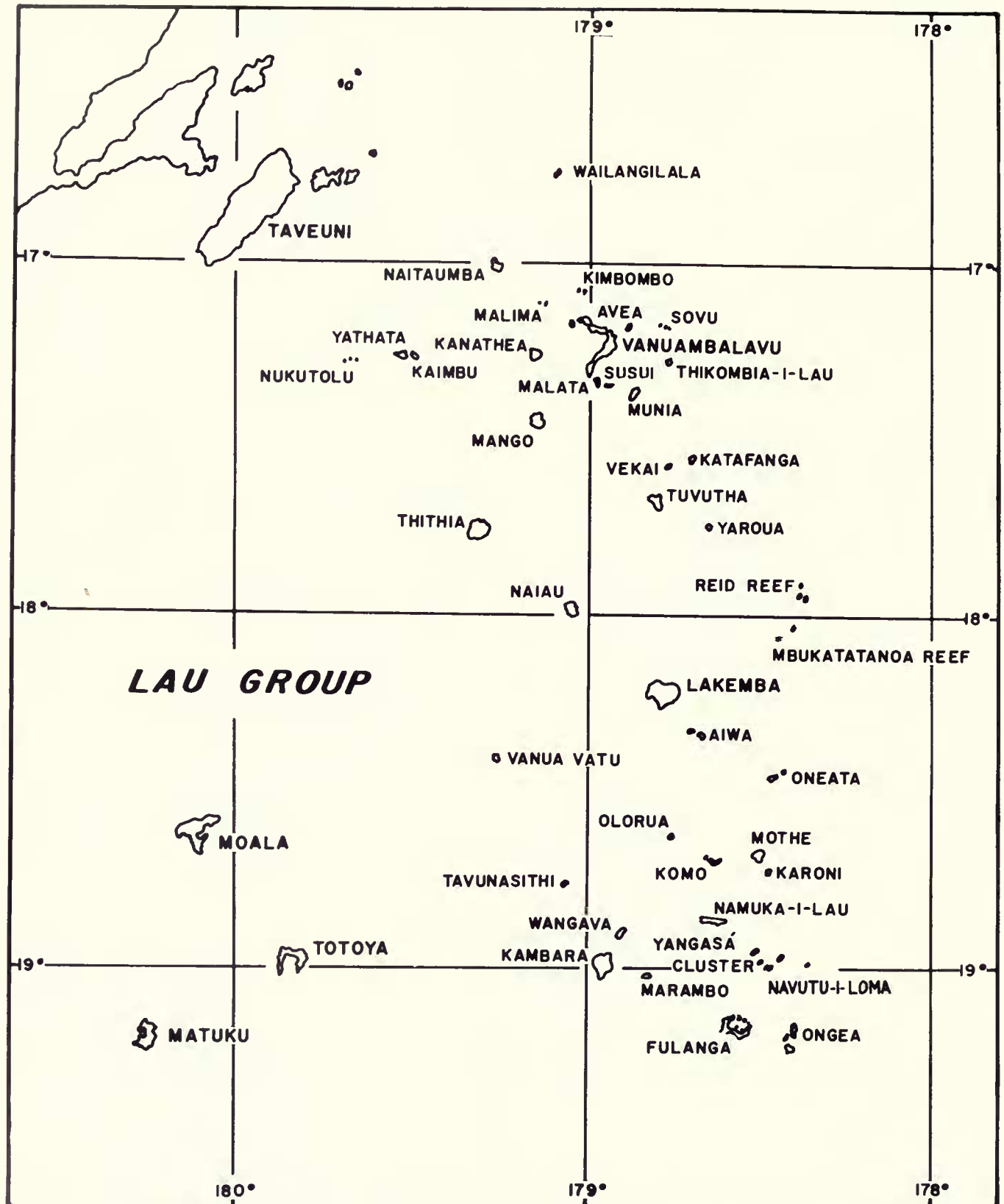


FIG. 125. Islands of the Lau Archipelago.

extant endodontoids are known from the Marshall Islands today. Their presence in former times is evidence added to that presented by Leopold (1969) that at least these two atolls were high islands with well-developed and heavy upland forests. The entire drilling sequences from Bikini, Eniwetok, and Midway (Ladd et

al., 1970) provided evidence of several thousand feet of sea floor subsidence during the Tertiary in the central Pacific. This is evidence that during the Late Tertiary the ranges of both the Endodontidae and Charopidae have contracted as the number of high islands present decreased and/or vanished from certain areas.



### Caroline Islands

The significant early collections from the Caroline Islands were summarized by Möllendorff (1900), based on collections made by Etscheid and Kubary in the 1890s. Most of the collections were on Ponape, but a few were from Yap and Truk. Subsequent collections in the mid-1930s by Kondo for the B. P. Bishop Museum and Thaanum in the 1940s complete the listing of available materials. With the exception of *Sinployea kusaieana* on Kusaie, all of the taxa belong to the endemic subfamily Trukcharopinae. *Trukcharopa* is reported from Truk and Lukunor, with the remaining eight species in six genera restricted to Ponape.

Local distribution patterns show that *Sinployea kusaieana* is widely distributed on Kusaie (fig. 126). The patterns of sympatry on Ponape were partially summarized in Table XLIV and can be more completely reviewed with use of the collecting locality map (fig. 127). Following this discussion, a list of the stations and number of specimens collected on Ponape is given.

*Trukcharopa trukana* is widely distributed within the Truk Group and is somewhat variable (tables XLVI, XLVII). The several collecting localities involved are shown in Figures 128–131.

The collection of the strongly differentiated genera known from Ponape is one of the more startling findings of this study. As mentioned above (p. 206), it is not feasible at this time to indicate phylogenetic relationships of these taxa. The general impression given by study of this group is of wide generic separation, accompanied by only minor specific diversification.

Station 91, west side of Tolomaim Mt. at 1,000 to 1,500 ft. elevation. T. Hirasawa and S. Ito. February 12, 1936.

*Jokajdon callizonus* (Möllendorff)—1

*Jokajdon tumidulus* (Möllendorff)—4

*Palikirus cosmetus* Solem—1

*Kubaryiellus kubaryi* (Möllendorff)—3

Station 92, 800 ft. elevation,  $\frac{1}{4}$  to  $\frac{3}{4}$  way up Mt. Tolotom. Y. Kondo, S. Ito, and natives. February 15, 1936.

*Russatus nigrescens* (Möllendorff)—2

*Roimontis tolotomensis* Solem—1

*Jokajdon callizonus* (Möllendorff)—1

*Jokajdon tumidulus* (Möllendorff)—2

*Kubaryiellus kubaryi* (Möllendorff)—1

Station 93,  $\frac{3}{4}$  way up to summit of Tolotom Mt. at 1,200 ft. elevation. Y. and K. Kondo. February 15, 1936.

*Russatus nigrescens* (Möllendorff)—11

*Roimontis tolotomensis* Solem—1

*Jokajdon callizonus* (Möllendorff)—9

*Jokajdon tumidulus* (Möllendorff)—27

Station 95, Wone, 900 ft. elevation, south side Tolotom Mt. Yoshio Kondo. February 16–17, 1936.

*Jokajdon callizonus* (Möllendorff)—1

*Jokajdon tumidulus* (Möllendorff)—14

Station 113, Paishapel hill, Metalanim at 650 to 700 ft. elevation. Y. and K. Kondo. February 27, 1936.

*Jokajdon callizonus* (Möllendorff)—1

*Kubaryiellus kubaryi* (Möllendorff)—14

Station 118, 450 ft. inland at 300 to 900 ft. elevation, Metalanim to Nipit trip. S. Ito. February 29, 1936.

*Jokajdon callizonus* (Möllendorff)—14

*Kubaryiellus kubaryi* (Möllendorff)—6

Station 121, side of Mt. Kuporujō at 500 to 900 ft. elevation. Y. Kondo. March 3, 1936.

*Jokajdon tumidulus* (Möllendorff)—1

*Kubaryiellus kubaryi* (Möllendorff)—1

Station 127,  $2\frac{1}{2}$  miles inland, southwest side of Toreairuku Mt. at 250 to 750 ft. elevation. S. Ito. March 7, 1936.

*Jokajdon tumidulus* (Möllendorff)—1

*Kubaryiellus kubaryi* (Möllendorff)—6

Station 129A, Nanalaut Mt., at 1,900 ft. elevation. Yoshio Kondo. March 7–8, 1936.

*Russatus nigrescens* (Möllendorff)—8

*Kubaryiellus kubaryi* (Möllendorff)—1

Stations 129 and 130, 1,600 to 2,500 ft. elevation, north slope of Nanalaut Mt. Yoshio Kondo. March 8, 1936.

*Jokajdon tumidulus* (Möllendorff)—3

*Kubaryiellus kubaryi* (Möllendorff)—2

Station 133, back of Naupilo. S. Ito and Y. Kondo. March 7, 1936.

*Jokajdon tumidulus* (Möllendorff)—11

*Kubaryiellus kubaryi* (Möllendorff)—4

Station 137, 450 ft. elevation,  $\frac{1}{4}$  mile south of school, Palikir. S. Ito and Y. Kondo. March 13, 1936.

*Palline micramyla* Solem—1

*Palikirus cosmetus* Solem—1

Stations 138 and 139, 600 to 900 ft. elevation, hillside on Jokaj Island. S. Ito and Y. Kondo. March 14, 1936.

*Jokajdon tumidulus* (Möllendorff)—1

*Palikirus cosmetus* Solem—5

*Kubaryiellus kubaryi* (Möllendorff)—3

Station 140, 1,000 to 1,250 ft. elevation, Mt. Tamantamansakir, Palikir. Y. Kondo and S. Ito. March 14, 1936.

*Jokajdon tumidulus* (Möllendorff)—6

*Palikirus cosmetus* Solem—1

*Kubaryiellus kubaryi* (Möllendorff)—6

### Mariana Islands

Despite the long history of these islands as a stopping point in trans-Pacific commerce, the only collections of land mollusks were made in the 1890s and reported on by Quadras & Möllendorff (1894). Archaeological investigations by members of the Bishop Museum staff in the 1920s and an expedition to Guam in 1949 by Bishop Museum staff members provide the data base for this study.

Except for a single record of *Sinployea* from Saipan, all of the Marianas taxa belong to the endemic subfamily Semperdoninae. Guam (fig. 132) has the endemic genera *Ladronellum* and *Himeroconcha*, the latter with a local radiation of four species. *Semperdon heptptychius* (Quadras & Möllendorff, 1894) is widely distributed on Guam, whereas *S. rotanus* is found on the northern tip of Guam and Rota Island. Probably both *Ladronellum* and *Himeroconcha* are locally evolved from *Semperdon*, whose distribution otherwise encompasses the Palau Islands.

The only situations involving sympatry are recorded from Guam, with a maximum of four species from the same locality. These are:

Guam, Mariana Islands, Ukudu, flat, under stones and logs, 2 miles from shore, 300 ft. elevation, in dense shade of native forest, on limestone soil, very dry. H. G. Hornbostel. November 10, 1925.

*Semperdon heptptychius* (Quadras & Möllendorff)—58

*Himeroconcha rotula* (Quadras & Möllendorff)—1

Mt. Lamlan, Guam, Mariana Islands; altitude 1,300 to 1,334 ft., hillside, dry, open forest, open ground, under stones, trash, on green leaves, branches, twigs, trunks of trees, on shrubs, dead leaves. H. Drucker, Bob Owen, Yoshio Kondo, Sydney Glassman, and Donald Anderson. September 4, 1949.

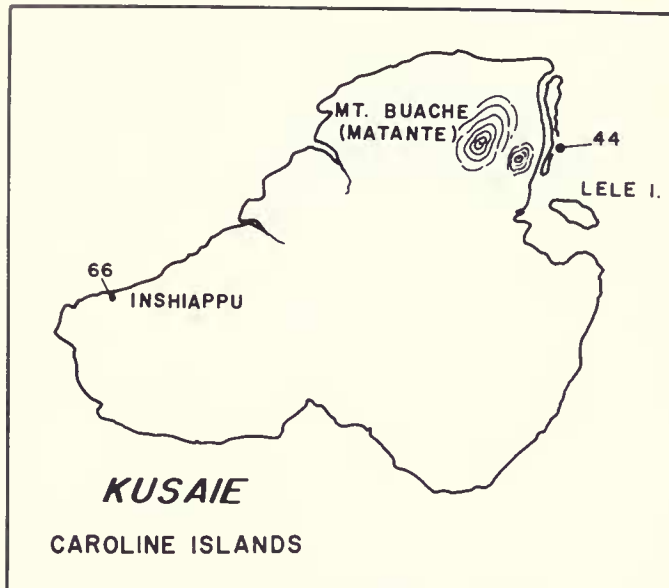


FIG. 126. Collecting localities on Kusaie, Caroline Islands. Micronesian Expedition, 1936.

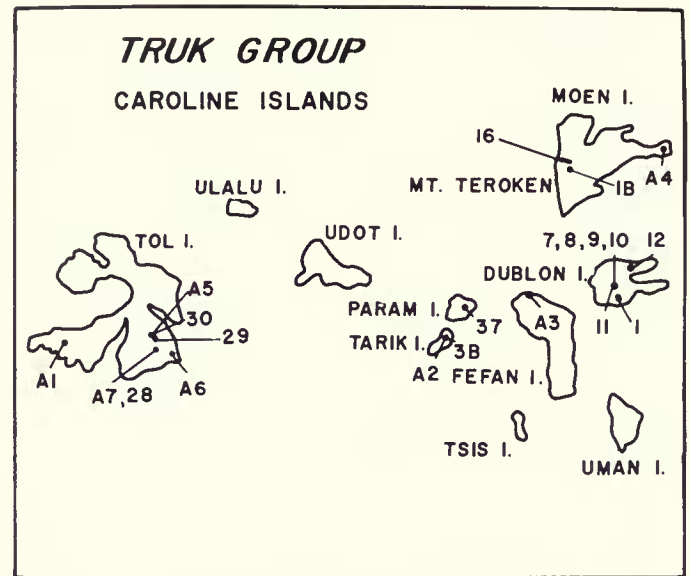


FIG. 128. Islets of the Truk Group, Caroline Islands.

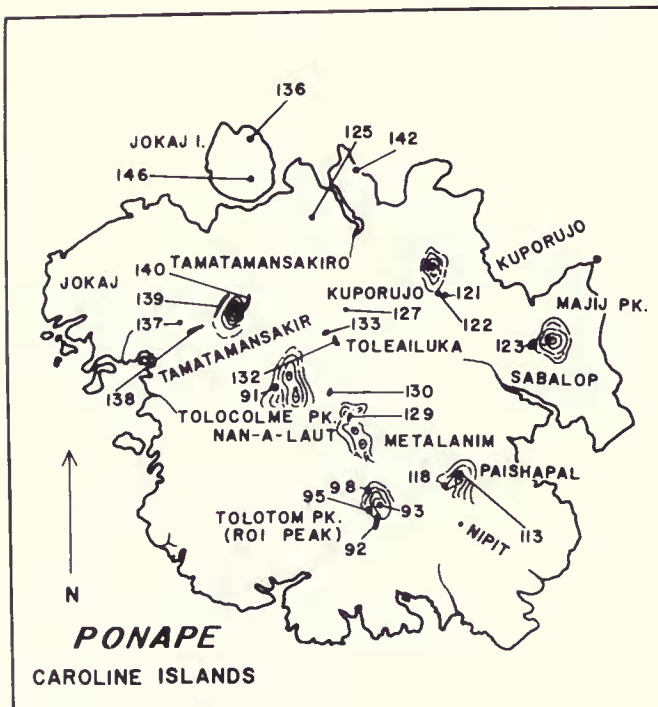


FIG. 127. Collecting localities on Ponape, Caroline Islands. Micronesian Expedition, 1936.

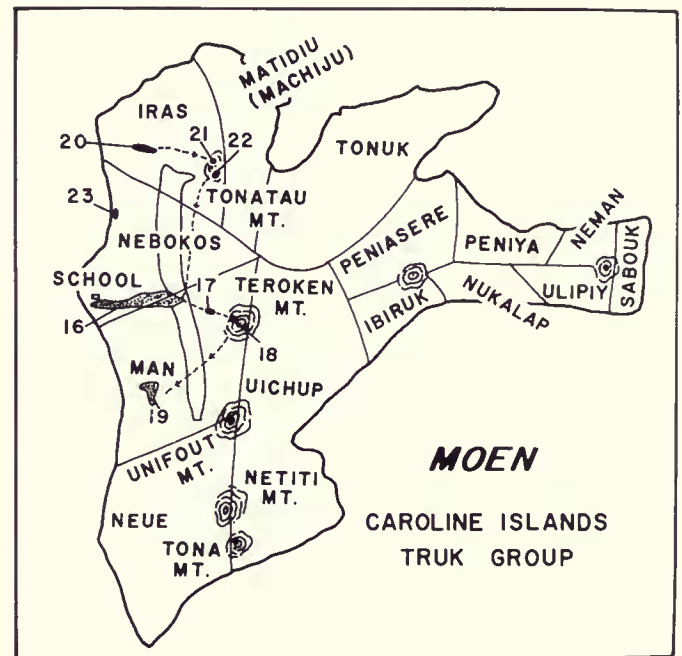


FIG. 129. Collecting localities on Moen Islet, Truk, Caroline Islands. Micronesian Expedition, 1936.

*Semperdon heptptychius* (Quadras & Möllendorff)—6

*Ladronellum mariannarum* (Quadras & Möllendorff)—15

*Himeroconcha lamlanensis* Solem—1

Mt. Lamlan, Guam, Mariana Islands; hillside, damp, open, and dense forest, under stones, trash, on green leaves, branches, twigs, shrubs, and dead leaves. Altitude 1,300 ft. Yoshio Kondo. October 28, 1949.

*Semperdon heptptychius* (Quadras & Möllendorff)—3

*Himeroconcha lamlanensis* Solem—1

*Himeroconcha fusca* (Quadras & Möllendorff)—23

*Ladronellum mariannarum* (Quadras & Möllendorff)—

112

Talofofo, Guam, Mariana Islands, Mata Cliffs; between cave and road on dirt way. Yoshio Kondo. October 26, 1949.

*Semperdon heptptychius* (Quadras & Möllendorff)—188

*Himeroconcha fusca* (Quadras & Möllendorff)—2

### Palau Islands

Semper (1874) described two species of the endemic genus *Aaadonta* from Peleliu, and Beddome (1889) described *Aaadonta fuscozonata* and *Semperdon*



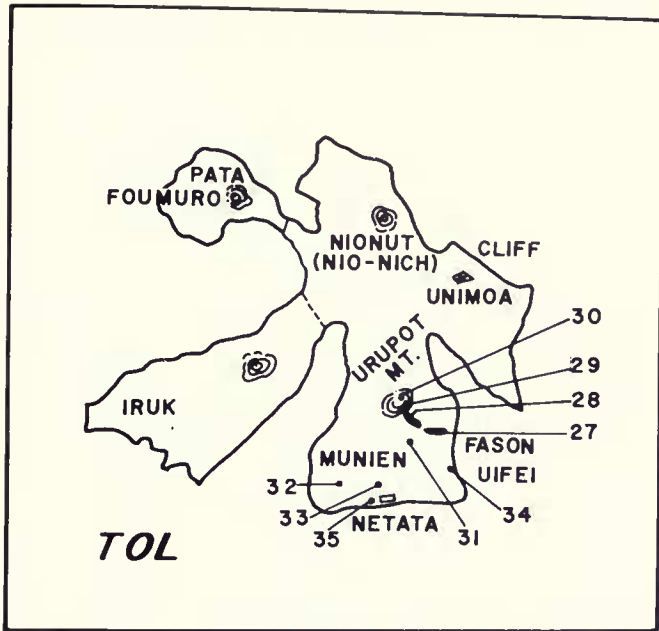


FIG. 130. Collecting localities on Tol Islet, Truk, Caroline Islands. Micronesian Expedition, 1936.

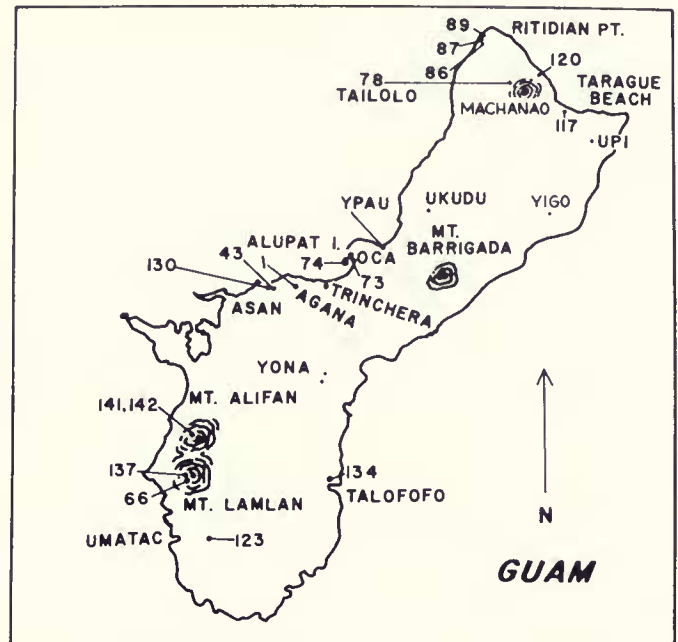


FIG. 132. Collecting localities on Guam, Mariana Islands. Various expeditions.

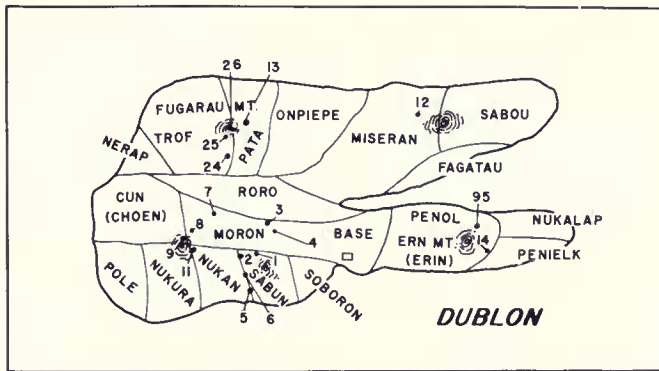


FIG. 131. Collecting localities on Dublon Islet, Truk, Caroline Islands. Micronesian Expedition, 1936.

*kororensis* from Koror. Highly significant collections were made by Kondo in the mid-1930s, which have been reported on by Solem (1976b) and above (pp. 205–245). The number of species-level taxa in *Aaadonta* was increased to nine. Three species of *Semperdon* and one species with three geographic races of the trukcharopinine genus *Palline* are known. Extraliminally, *Palline* is also found on Ponape and Biak, whereas *Semperdon* is found on Guam and Rota. *Aaadonta* is very closely allied in anatomy to *Thaumatodon*, *Priceconcha*, and *Zyzyxdonta* from Fiji and adjacent islands. Thus, Palau has an endodontoid fauna composed of at least three separate colonizations, which show quite different geographic affinities.

The general aspect of the Palau Group is indicated in Figure 133. Almost no collecting has been done on the large island of Babelthup. In contrast, several localities have been recorded on Peleliu (fig. 134) and Koror (fig. 135). Although only a single station was

made on Angaur (fig. 136), four species, including two restricted to that island, have been recorded.

No recent collections have been made, so that the extent of extinction remains unknown. On Koror, a maximum of five species (Station 203) has been taken sympatrically, whereas on both Peleliu and Angaur, four species have been collected together. A summary of the joint occurrences follows.

#### BABELTHUP

Station 15, limestone hillside, 30 m. inland at 20 to 40 m. elevation, Airai-mura, Adelulu hill. S. Ito and native. April 21, 1936.

*Aaadonta constricta babelthuapi* Solem—3

*Palline notera gianda* Solem—10

#### AULUPTAGEL

Station 230, hillside at 5 to 90 ft. elevation. S. Ito and Y. Kondo. May 12, 1936.

*Semperdon uncatus* Solem—1

#### KOROR

Station 212, 10 yd. inland at 30 to 100 ft. elevation, northeast side, western neck of Islet XXXIX. S. Ito and Y. Kondo. May 5, 1936.

*Palline notera palauana* Solem—2

*Semperdon xyleborus* Solem—2

Stations 217 and 219, south of and below Station 218, 50 to 75 yd. inland at 75 ft. elevation, Komakan. Y. Kondo. May 9, 1936.

*Aaadonta fuscozonata fuscozonata* (Beddome)—20

*Palline notera palauana* Solem—1

*Semperdon xyleborus* Solem—17

Station 221, 1 to 150 ft. inland at 5 to 90 ft. elevation, southeast end of peninsula, Komakan. Yoshio Kondo. May 11, 1936.

*Aaadonta constricta komakanensis* Solem—42

*Aaadonta fuscozonata fuscozonata* (Beddome)—12

Station 222, above Station 221 at 100 to 200 ft. elevation, Komakan. Yoshio Kondo. May 2, 1936.

*Aaadonta fuscozonata fuscozonata* (Beddome)—3

*Semperdon kororensis* Solem—11

*Semperdon uncatus* Solem—1

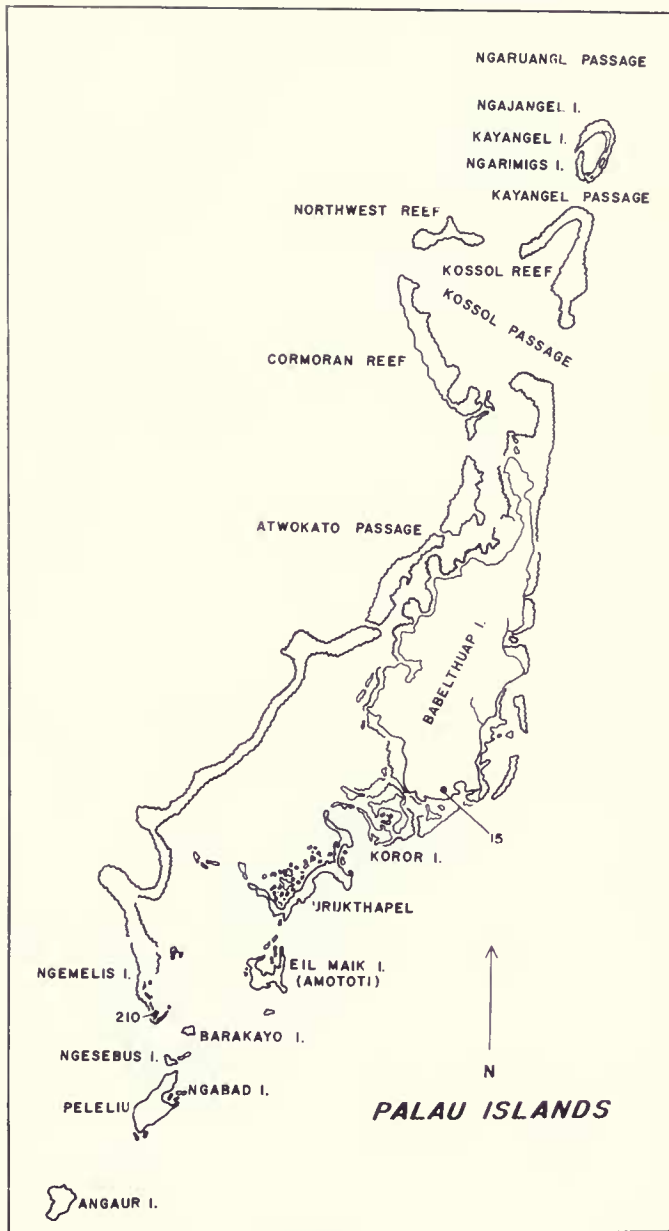


FIG. 133. Islands of the Palau Group.

In forest on limestone. E. V. Hosaka. July 20, 1946.

*Palline notera palauana* Solem—1

*Semperdon xyleborus* Solem—1

#### NGEMELIS

Station 210, hillside at 2 to 35 ft. elevation on #8 islet. Y. and K. Kondo and natives. May 2, 1936.

*Aaadonta constricta babelthuapi* Solem—1

*Semperdon xyleborus* Solem—13

#### PELELIU

Station 182, hillside  $\frac{1}{2}$  to  $\frac{3}{4}$  mile inland at 300 to 400 ft. elevation, Asias Village, Omurbrogol Mt. Y. and K. Kondo and Sanborn. April 23, 1936.

*Aaadonta constricta constricta* Semper—27

*Aaadonta irregularis* Semper—2

*Palline notera notera* Solem—4

*Semperdon xyleborus* Solem—5

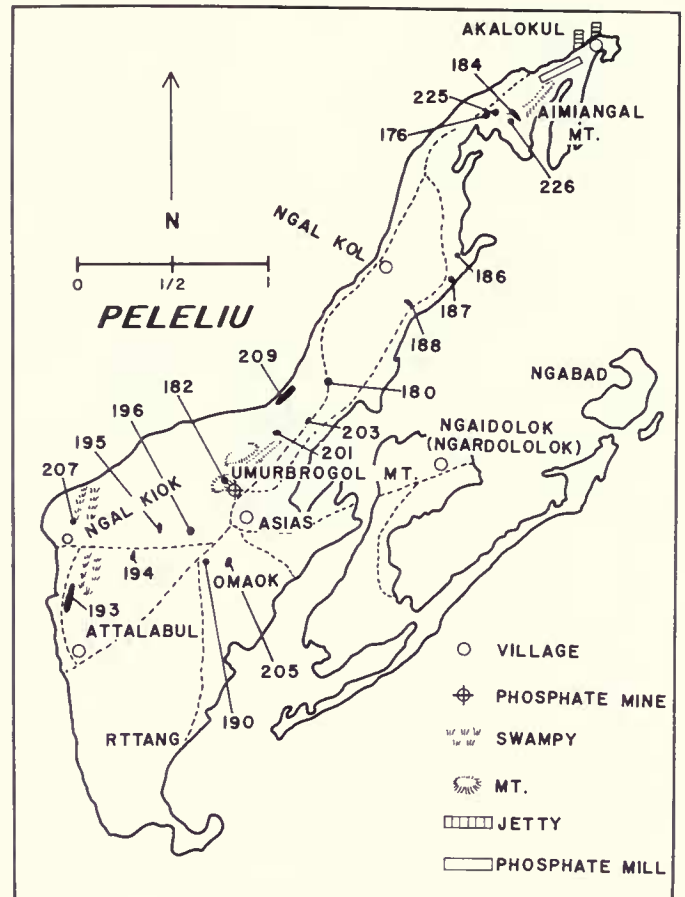


FIG. 134. Collecting localities on Peleliu, Palau Group. Micronesian Expedition, 1936.

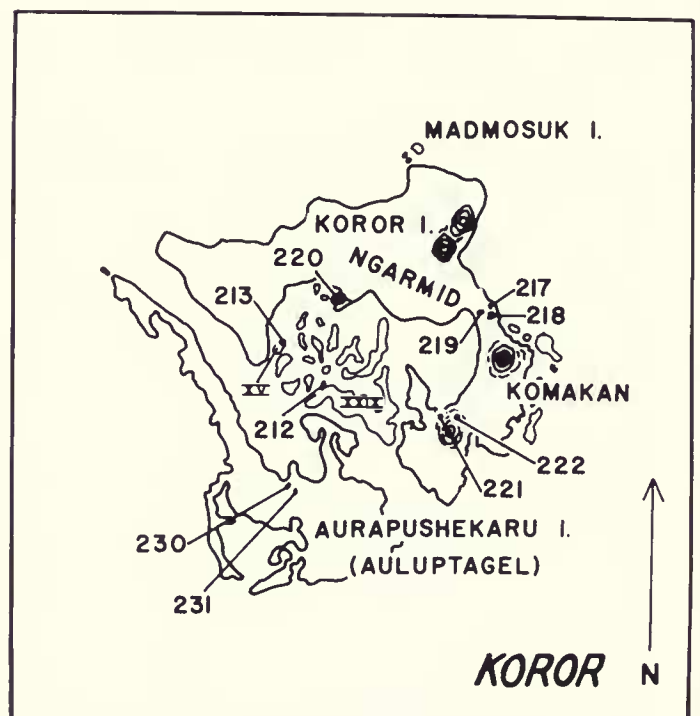


FIG. 135. Collecting localities on Koror and Auluptagel, Palau Group. Micronesian Expedition, 1936.



Station 184, damp hillside 100 yd. inland, east of Station 176 at 200 ft. elevation. Y. and K. Kondo and Atietho. April 24, 1936.

*Palline notera notera* Solem—1

*Semperdon xyleborus* Solem—33

Station 201, hillside north of phosphate mine at 35 to 200 ft. elevation. Y. Kondo and natives. April 29, 1936.

*Aaadonta constricta constricta* (Semper)—51

*Aaadonta irregularis* (Semper)—2

*Palline notera notera* Solem—42

*Semperdon xyleborus* Solem—7

Station 203, hillside 300 to 400 yd. north of Station 201. Y. Kondo and natives. April 29, 1936.

*Aaadonta constricta constricta* (Semper)—1

*Aaadonta fuscozonata depressa* Solem—2

*Aaadonta irregularis* (Semper)—2

*Palline notera notera* Solem—1

*Semperdon xyleborus* Solem—1

#### ANGAUR

Station 175, edge of guano pit north of shrine at 75 to 100 ft. elevation. Y. and K. Kondo. April 18, 1936.

*Aaadonta angaurana* Solem—128

*Aaadonta kinlochii* Solem—173

*Semperdon uncatus* Solem—13

*Semperdon xyleborus* Solem—90

#### SUMMARY OF SPECIFIC AND GENERIC DIVERSITY

The overriding fact of endodontoid specific and generic diversity within the Pacific Basin is the high degree of endemism. This applies as well to extralimital areas as to the areas revised in this report. In respect to just Micronesia (Palau, Caroline, Mariana, Marshall, and Gilbert Islands), Polynesia (Ellice Islands, Rotuma, Lau, Futuna, Tonga, Samoa, and islands east to Henderson Island, plus Hawaii), and the

main islands of Fiji, which generally are considered to be part of Melanesia, none of the 25 genera of Endodontidae extend extraliminally. The single Polynesian genus of the Punctidae, *Punctum*, is basically Holarctic, with a minor radiation in Hawaii, then isolated occurrences in Tahiti and the Austral Islands. The Charopidae show a somewhat less restricted pattern of distribution, with one genus, *Discocharopa*, widely distributed outside of the study area (west to Philippines, Indonesia, and Northern Australia), and three genera, *Palline*, *Lagivala*, and *Sinployea*, at least marginally represented in Melanesia and/or New Guinea. The remaining 16 genera of Charopidae are restricted to the study area.

At the species level, the degree of endemism is even higher. All of the 190 species-level taxa of Endodontidae, 87 species of Charopidae, and probably the few species of *Punctum* occur only within these limits. Of the 290 species-level taxa recorded in these studies, only *Discocharopa aperta* (Möller, 1888) extends extraliminally.

The exact degree of specific endemism of the Achatinellidae-Tornatellinidae lineage cannot be determined because Cooke & Kondo (1960) and Kondo (1962) did not have sufficient material to formally revise the various nominate taxa recorded from extralimital fringe areas. It is probable that most, if not all of these, will be found to be based upon introduced populations of widespread Polynesian and Micronesian taxa because specimens of these genera are routinely collected from the leaves and stems of garden plants and subsistence crops. On the generic level, however, the Achatinellidae-Tornatellinidae show nearly equivalent endemism (Cooke & Kondo, 1960, p. 24, table 1; Solem, 1972b). There are 13 genera (including *Tekoulinea*, Solem, 1972b) that are restricted to only one island (nine of these to Rapa), nine other genera occur only in one archipelago, and only five genera show a moderate to wide distribution.

A somewhat contrasting picture is presented by the Helicarionidae and Zonitidae. As pointed out by H. B. Baker (1940, p. 347) one "... must take into consideration the probability that they are the most advanced families of terrestrial mollusks which have endemic species in most parts of the Pacific region." He reported that 95% (253 of 266) of the species, but only 35% (12 of 32) of the genera, were limited to the study area. Of the genera with restricted ranges, *Philonesia* and *Hiona* have extensive eastern Polynesian ranges, including Hawaii and Rapa, plus the Marquesas and Tuamotu, whereas *Microcystis* is restricted to the Austral and Cook Islands. The remaining nine genera are found only on a single island or in a single group. The zonitid genus *Godwinia* is restricted to Kauai, the helicarionids *Kaala* to Oahu, *Pukaloa* to Raiatea, Society Islands, *Mendaña* to the Marquesas, and *Cookeana* to Tubuai, Austral Islands. The remaining genera represent a Caroline Islands radiation equivalent to the Trukcharopinae, except centered on Truk rather than

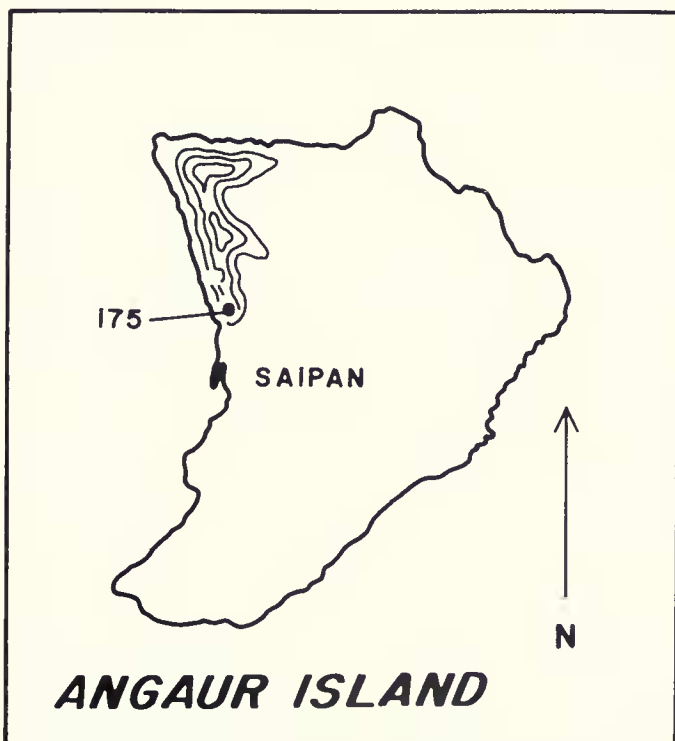


FIG. 136. Collection Station on Angaur, Palau Group. Micronesian Expedition, 1936.

Ponape. The trochomorphid genera, *Kondoa*, *Hogolua*, and *Brazieria* from Truk, with the latter genus also recorded from Lukunor, plus the microcystine genus *Kusaiea* from Kusaie and Truk represent endemic genera. The subgenera *Trukrhysa* from Truk and *Ponapea* from Ponape represent markedly differentiated subgenera of more widely distributed taxa. Although the generic endemism of the helicarionid-zonitid stocks in the Pacific is less marked than for the other taxa, it nevertheless represents a strong endemic element.

On the basis of collections preserved in the Bernice P. Bishop Museum, it is known that there are extensive radiations of Diplommantinidae and Assimineidae in Micronesia and parts of Melanesia, many pupillids and succineids in various parts of the Pacific, and the incredible Hawaiian radiation of Amastridae. Unfortunately, modern species-level revisions of these taxa have not been accomplished, and data on their actual diversity levels and degree of endemism remain unavailable.

In complete contrast to the pattern shown by the vertebrates and in strong contrast to that of most insect taxa, the land snails of Micronesia and Polynesia show an incredible degree of endemism at both the species and generic level.

With the above background information, it is possible to summarize the patterns of specific and generic diversity for the endodontoids.

Figures 137 and 138 indicate diversity in the Endodontidae and Charopidae as recorded by Solem (1976b; 1977a; in preparation B; and this report). Figure 137 summarizes the number of recent and fossil species in the two families known from each archipelago. The actual diversity in Hawaii obviously is grossly under-represented (see data on undescribed taxa in tables LXVI–LXVII) and simply represents named and published taxa. The only areas of the Pacific in which the two families were present in anywhere near equal diversity are the Palau and Cook Islands. Although Tonga, Lau, Samoa, and the Society Islands have representatives of both families, they are not present there in approximately equal numbers.

There is no question that the major species-level diversity was found in eastern Polynesia—Hawaii, Marquesas, Tuamotu, Mangareva, Rapa, Austral, Society and Cook Islands—areas where the Endodontidae were dominant. Secondary foci of diversity included Palau, Marianas, Ponape, Samoa, and Fiji, with two geographically intermediate areas—the Lau Archipelago and Tonga—showing high species numbers. It must be emphasized again that for practically none of these areas do we have comprehensive knowledge of what the total extant fauna might have been as late as 1850. These numbers represent undoubted underestimation of the evolutionary achievement of these families.

There is no indication, based on the known extent of sympatric occurrences, that the Charopidae tend to

displace the Endodontidae in areas of range overlap. On Upolu (see p. 292) and on the Society Islands (see pp. 288–289) for example, species of both families were taken abundantly at the same stations. The Endodontidae were almost exclusively dwellers in the ground litter, especially under rocks and fallen logs or palm fronds. The main genus of the Charopidae found in the Lau Archipelago to Society Islands zone of overlap, *Sinployea*, includes many species collected from stilt roots and on tree trunks, thus occupying a semi-arboreal habitat and being at least marginally ecologically separated from the Endodontidae. In both Samoa and the Society Islands, members of the Charopidae have been personally collected under relatively ecologically disturbed conditions. The absence of Endodontidae from the same stations reflects other biotic factors, such as litter disturbance or predation by introduced ants.

Figure 138 summarizes raw data on the known level of generic diversity. The presence of nine genera in Lau; eight in the Caroline Islands; six in the Cook Islands; five in Fiji, the Society Islands, and Rapa; and four in Mangareva, Austral Islands, Ellice Islands, and the Mariana Islands indicates the major areas of diversification. As pointed out earlier (pp. 268–269), a high percentage of the genera are restricted to single islands or at most to a single archipelago.

It is instructive to view these levels of diversity from the standpoint of the minimum number of colonizations that would be required. For Hawaii, the Marquesas, and Rapa, one colonization by a generalized member of the Endodontidae could have led to their current diversity. For the Tuamotu, Cook, and Mangareva, either two or three colonizations may have been required. Thus, most of the high-diversity areas in eastern Polynesia represent *in situ* radiations from a highly limited number of introductions.

For the Society and Austral Islands, where different families are involved, an independent introduction for each family would be needed, but within each family unit, local diversification could have proceeded from a single successful colonization. It is only when considering such areas as Samoa, Tonga, and Lau (minimum of five colonizations), Viti Levu, and the Ellice Islands (minimum of four colonizations) that multiple invasions or the less probable factor of vicariance phenomena must be accepted. With regard to Micronesia, the fossil record from the Marshall Islands suggests three separate colonizations; and the Palau, Caroline, and Mariana Islands also suggest two or three separate colonization events.

In summary, for none of the islands in Micronesia, Polynesia, and Fiji is it necessary to postulate more than five or six successful colonizations by endodontoid land snails to be followed by local speciation and generic diversification. Such events would account for the discovered level of diversity in the endodontoid land snails.



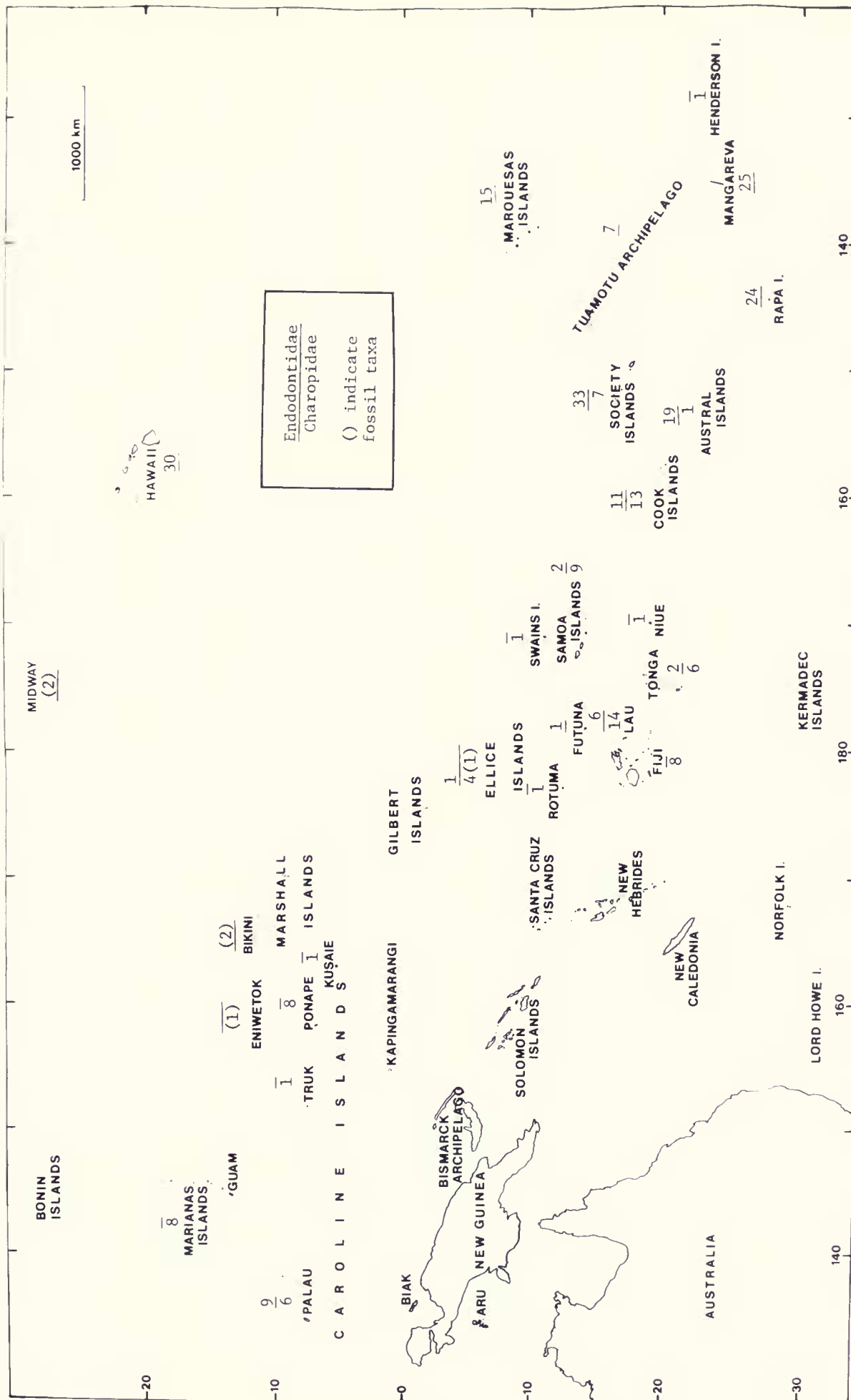


Fig. 137. Species diversity in island groups for the Endodontidae and Charopidae. Hawaiian radiation grossly underestimated because the vast majority of the taxa are undescribed.

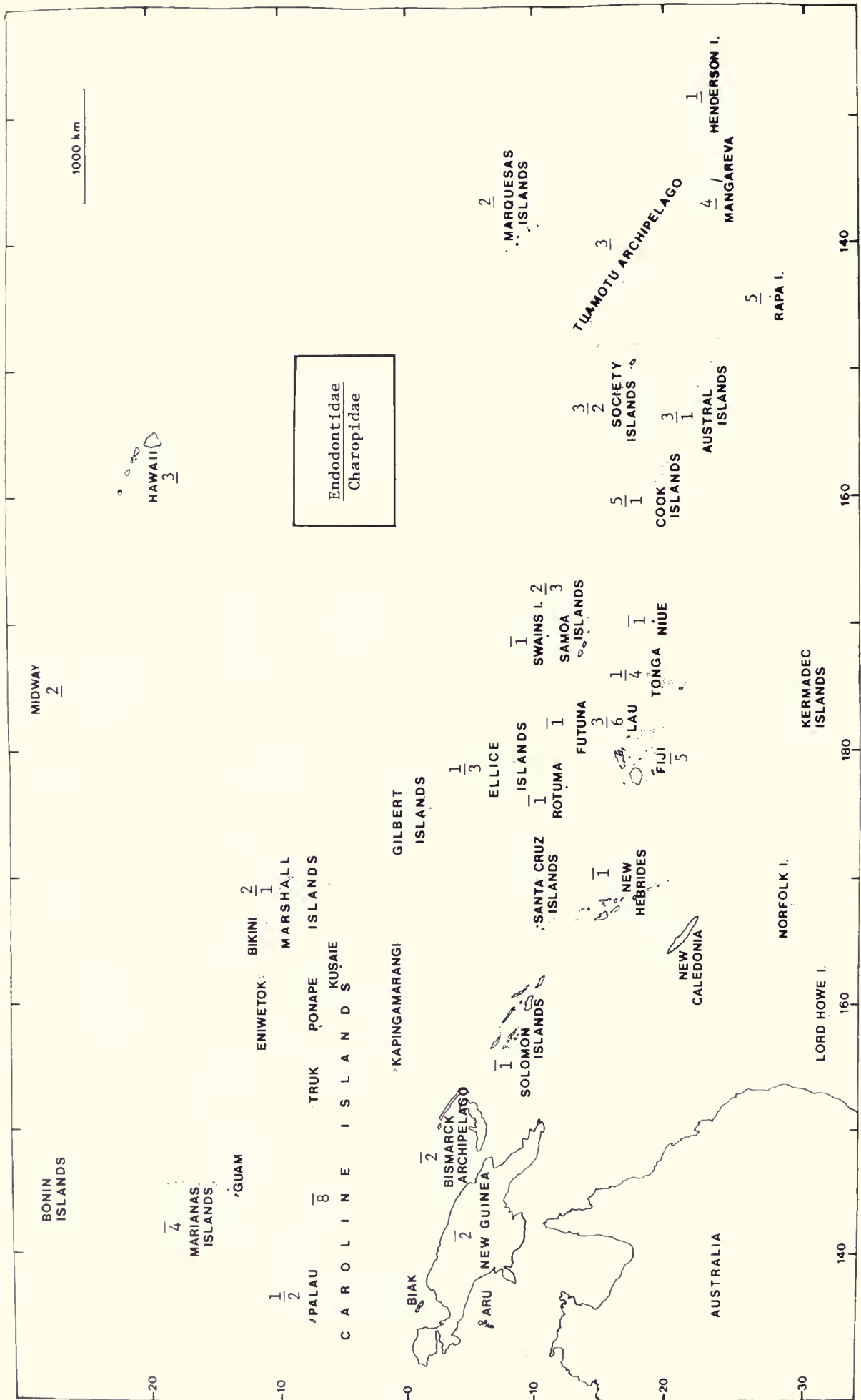


FIG. 138. Generic diversity in island groups for the Endodontidae and Charopidae. Generic limits for the Hawaiian taxa are broader than those from other areas because so much of the radiation is undescribed.



## SHELL SIZE AND GEOGRAPHY

Figure 139 attempts to summarize the geographic patterns of endodontoid adult shell size in relation to geography. For each island group I present the median mean shell diameter of adult specimens as an indication of size. This figure is followed by the range in mean adult shell diameters for that island group. The numbers of measured Endodontidae and Charopidae for that area are indicated in parentheses. Wherever an even number of data points resulted in a spread between means, the median has been averaged between the two middle points. So little material is available from the Pacific Basin for the Punctidae that this taxon has been omitted from this review. The use of the median mean shell size has been chosen to avoid the skewing of data that would result by averaging in the very large "brood chamber" and *Nesodiscus*-level taxa found in Eastern Polynesia.

Several patterns can be distinguished after presentation of some background data. First, there is an area of the Pacific in which the endodontoids form a very minor element of the land snail fauna. From New Guinea through the New Hebrides to the main islands of Fiji, only members of the Charopidae have been reported (except some high-mountain Punctidae in New Guinea). Nowhere are they abundant in numbers or very speciose. None of the charopid species from this area reviewed in this report exceed 2.87 mm. in mean adult diameter. Most of them are well under 2.3 mm. in diameter and range down to 1.07 mm. in adult size (*Microcharopa*). The few species of *Sinployea* are the smallest in size (p. 166) for the genus. The situation is slightly complicated by inclusion of Indonesian-Melanesian taxa not covered in this monograph. The New Hebridean endemic *Reticharopa* Solem (1959b, pp. 85–88) averages only 2.4 mm. in mean adult diameter. The New Guinea endemic genera *Pilsbrycharopa* and *Paryphantopsis* (Solem, 1970a) include small (*Pilsbrycharopa kobelti*, mean diameter 2.06 mm.) to large (*P. gressitti*, Solem, 1970, mean diameter 6.76 mm.) shells. The small- and medium-sized species of *Pilsbrycharopa* are recorded from Bali, Sumbawa, Timor, Misool, Ambon, and Sabah; the larger species are known from New Guinea and the Bismarck Archipelago. *Paryphantopsis* Thiele, 1928, which is restricted to New Guinea, ranges in adult size from 3.6 to 12.0 mm. in diameter, but with only 2¾ to 4½ whorls. It is an experiment in visceral hump reduction, representing an early stage in evolution toward a slug. These two Indonesian-New Guinea genera are not closely related to any taxa reviewed here and thus do not alter the basic pattern of minute species in the geographic area of New Guinea through Fiji.

As indicated by Solem (1961, pp. 451–470) the New Caledonian radiation includes the largest known endodontoids, with some specimens of *Pararhytida dictyodes* (Pfeiffer, 1847) exceeding 40 mm. in diameter. The affinities of this radiation have not yet been worked out, but dissections done so far (Solem, unpub-

lished data) indicate that they are not closely related to the Pacific Island taxa.

For most of the island groups in Micronesia and Polynesia the smallest species of endodontoids are less than 2.2 mm. in mean adult diameter. Exceptions to this in the two families will be considered separately. In the Palau Islands, *Aaadonta* represents the structurally most advanced genus of the Endodontidae. It has radiated into nine species-level taxa. At the opposite end of the Pacific, the radiation known from Makatea, Tuamotu Archipelago, consists of species that are highly derived and, because of their specializations, they must be large in size. Similarly, in the Society Islands, the partly known portion of the endodontid fauna consists of highly derived (*Nesodiscus*-level and brood chamber) genera, plus the extensive radiation of *Mautodontha*. No Society Island members of the basic and small *Minidonta-Cookeconcha* stock are known. Tonga and the Ellice Islands have only a few members of the quite advanced genus *Thaumato-**don*. The absence of small endodontids from the Marquesas may be an artifact of collecting. Because of the great destruction and relatively limited collecting done in these islands, it is impossible to give a reasoned opinion on this.

Except for the Cook, Tonga, and Mariana Islands, which lie near the fringes of the Charopidae distribution, all of the islands contain at least some small-sized species. The presence of only larger taxa in these fringe areas parallels the general situation in the Endodontidae, in that the islands lying near the outer fringes of the family distribution tend to have distinctly larger median mean adult sizes than those islands that lie near the Melanesian "core." No sophisticated statistical treatment of the above data has been attempted, but the pattern of size increase on the outer islands is obvious from the data in Figure 139. Exceptions, such as Henderson Island with the one species and the presence of only minute species as fossils in the Marshall Islands, do not alter the basic pattern of size increase in the outer areas.

This undoubtedly relates to factors of local speciation, with the tendency toward evolution of large size from a probable small ancestral form. Because the "core area" of Melanesia is basically inhabited by genera with wider distribution, whereas the outer islands have primarily endemic genera, such a pattern would be expected.

This is contrary to the opinions put forth by Vagvolgyi (1976) that also have been criticized on other grounds by Platnick (1976) and Croizat (1978). Further reference to the controversy is made below (p. 308).

To summarize the above, large endodontoid snails have evolved independently on the outer islands of the distribution range, most probably from very small-sized colonizers. The New Guinea to Fiji area is characterized by small species of rather widely distributed genera that are not speciose and locally are relatively rare.

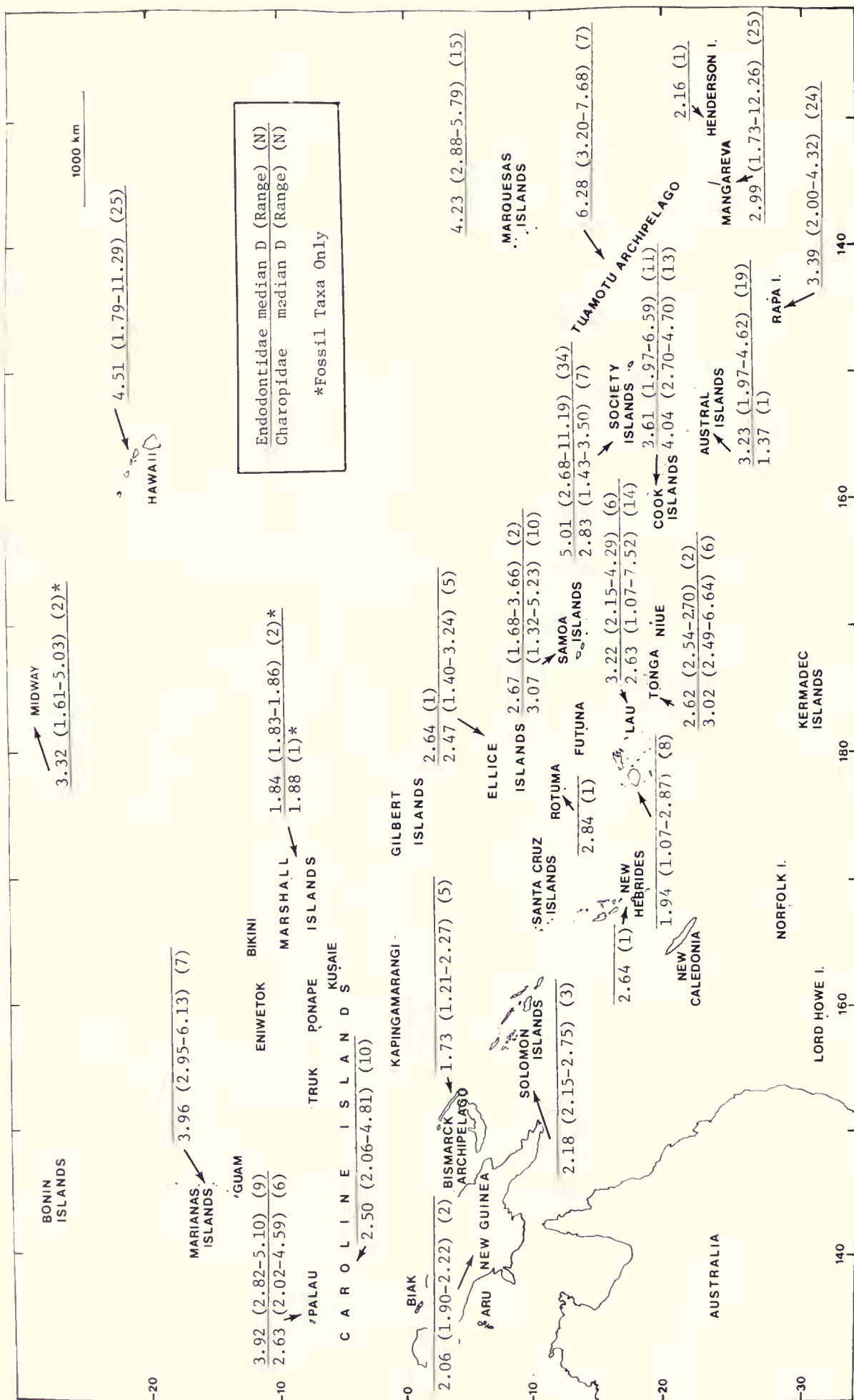


FIG. 139. Median mean and mean ranges of adult shell diameter in island groups for the Endodontidae and Charopidae. The single record of *Sinployea* from the Marianas has been omitted because the specimens are subadult.



The most reasonable explanations for the absence of larger endodontoids from most of the New Guinea to Fiji area would involve factors of biological competition or predation. Possible snail competitors cannot be pinpointed. Diplommantinids and assimineids coexist with the charopid radiation in Palau, Carolines, and Lau, whereas the large trochomorphids and many helicarionid taxa are common throughout much of the Pacific. It is highly dubious that the very large papuinids and bulimulids (*Placostylus*, s. l.) could have any effect upon the minute endodontoids.

A more likely explanation involves predation, with the most likely culprits being ants. An abundant and diverse fauna of native ants extends as far east as Fiji, and a few endemic ant species have been described from the large islands of Samoa (Wilson & Taylor, 1967b). Although members of *Sinployea* seemingly have survived the introduced ants in eastern Polynesia, the endodontoids apparently have not. Quite possibly other arthropod predators are involved in the restriction of adult size among Melanesian charopids, but this is speculation.

#### HYPOTHESIZED ORIGIN AND RADIATION OF PACIFIC ISLAND ENDODONTOID SNAIL FAUNA

Any theory as to the time and area of origin for a fauna must be consistent with the known facts as to the habitable geologic age of the area and the antiquity of the organisms involved. Only partial data on both points is available for the Pacific Islands.

When my previous major review of Pacific land snail biogeography (Solem, 1959b) was written, little geologic data were available concerning the actual ages of individual islands. It was possible to state, on the basis of work done by Harry Ladd (1957, 1958) and various pioneer seafloor surveys that had revealed scattered seamounts, that "The Bikini core drillings and the numerous guyots in the mid-Pacific indicate that there have been substantial subsidence of the Pacific Ocean floor in the Tertiary Period. Although almost none of the present high islands have been in existence for more than a fraction of the total history of the area, it is not unreasonable to suppose that there may have been isolated high islands in the Pacific. . . ." (Solem, 1959b, p. 325). Subsequently, the classic summary of Pacific paleogeography by Menard & Hamilton (1963) and a large number of potassium/argon datings have provided rather comprehensive data. It is evident that many of the islands are far older than would have been allowed by Zimmerman (1948) or Gressitt (1961). Many of the dates require further confirmation, and between the time of writing this and publication, the actual data base probably will shift, but the overall pattern seems well established.

Dating by reef fossils, potassium/argon dating of volcanic rocks, and even the dating of coal deposits have been used by various authors. The results are not necessarily compatible (see Clague & Jarrard, 1973, ta-

bles 1 and 2), and estimates on particular islands can vary widely. Thus Rapa has a potassium/argon date of 5.2 m.y. (see table LXX), but Clarke (1971, p. 5) indicates that it "was probably formed as early as the Eocene," and its coal samples have been dated from 1,000,000 to 25,000,000 years old.

Table LXX summarizes available potassium/argon data on island ages from the outer Pacific. In particular, the summary of Clague & Jarrard (1973) is helpful. The age sequence in Hawaii is now well accepted (see Stearns, 1978a, b), but the age of Tahiti and Moorea remains uncertain. The early estimate of Krummeracher & Noetzelin (1966), yielding a potential age of 156 m.y. for Tahiti, was not confirmed by Dymond (1975), whose more conservative estimates are accepted here. The assignment of ages in excess of 30 m.y. to such islands as Makatea, Mangareva, Bikini, Eniwetok, and Guam provides a long-term basis for habitation of the Pacific Islands that was lacking 20 years ago.

The question of biologically habitable age is, of course, unanswerable at present. The assignment of a

TABLE LXX. - AGES OF PACIFIC ISLANDS

Islands	Age in Millions	Source of Dating
Hawaiian		
Hawaii	0.68	Dalrymple (1971)
Maui	1.30	McDougall (1964)
Molokai	1.84	Same
Oahu, Koolau	2.55	Jackson, <u>et al</u> (1972)
Oahu, Waianae	3.6	Same
Kauai	5.6	Same
Midway	17.9	Clague and Jarrard (1973)
Marquesas		
Fatu Hiva	1.3	Brousse, <u>et al</u> (1978)
Eiao	6.3	Same
Tuamotu	75 - 80	Winterer, <u>et al</u> (1971)
Makatea	37.5-53.5	Repelin (1919)
Austral		
Rapa	5.0-5.2	Krummeracher & Noetzelin (1966)
Raivavae	14.1	Same
Tubuai	24.9	Same
Mangareva	38	Brousse, <u>et al</u> (1974)
Society		
Tahiti	1.4	Dymond (1975), Stearns (1978a)
Moorea	1.65	Same
Cook		
Rarotonga	2.8	Tarling (1967)
Marshall Islands		
Bikini	37.5-53.5	Emery, <u>et al</u> (1954)
Eniwetok	59	Kulp (1963)
Caroline Islands		
Truk	9-22.5	Stark, <u>et al</u> (1958)
Marianas Islands		
Guam	50+	Tracey, <u>et al</u> (1964)

high potassium/argon age to volcanic rocks tells nothing about when the island became habitable to present occupants, but does give a general framework against which to discuss colonizations. With regard to island areas that showed a great diversity in the endodontoids, Rarotonga (2.8 m.y.), Rapa (5.2 m.y.), Waianae area of Oahu (3.6 m.y.), and even Tahiti (1.4 m.y.) supported extensive species and generic radiations, whereas the Koolau area of Oahu (2.55 m.y.) did not. We have no knowledge as to when each of these islands became habitable by endodontoids, much less when the actual colonization occurred, but the above ages do give a rough time figure against which to speculate.

The summary statement of Tracey et al. (1964, p. A95) that "It seems likely that a general subsidence of the Central Pacific basin starting in middle or Late Cretaceous time may be related to the early states of formation of the arcs around the basin, and that the Mariana geanticline therefore may have started forming in late Mesozoic rather than early Cenozoic time," coupled with the wide distribution of guyots (Menard & Hamilton, 1963), provides a geologic framework. In the Late Mesozoic the Central Pacific had a larger number of islands than now exist in this region. Many of these were high volcanic islands capable of supporting a diversified fauna and flora. The present pattern of atolls in much of the Pacific thus is a secondary phenomenon. The reduction in number of high volcanic islands has resulted in a steady impoverishment of the Pacific biota, such as the extinction of endodontoid land snails from the Marshall Islands and Midway.

The actual age to be assigned the land snail taxa of the Pacific Basin has been controversial. The early speculations of such authors as Pilsbry (1900a, b, 1916, 1921), Cooke (1926), and Germain (1932, 1934), who proposed a "mid-Pacific continent," were based on the presence of land snail families endemic to Polynesia that are quite primitive in structure. They did not have any direct fossil evidence. The latter lack has changed in recent years. Solem & Yochelson (1979) reviewed the Paleozoic land snails and the ecological bases for land snail origins. They determined: that the Paleozoic land snails all can be referred to extant families, that the Stylommatophora are substantially older than the Basommatophora, and that the land snails show very conservative distribution patterns through time (Solem, 1979b). These data lead to major changes in contemporary thinking. The theory of Vagvolgyi (1976) that the land snails on the Pacific Islands all are of recent origin is not supported by this newly available evidence.

The actual time of origin for nearly all land snail families is unknown. At their time of first appearance in the fossil record most families are fully differentiated (Solem, 1979a), and very few fossils cannot be assigned to an extant family. Although we can date the time of fossil record appearance for many groups, their actual time of origin, place of origin, and ancestral

group remain unknown. Three of the six extant orders of land snails are found in the Paleozoic, and the other shell-bearing taxa appear by the Paleocene (Solem & Yochelson, 1979). The tornatellinid-achatinellid lineage dates back to the Pennsylvanian, with a range including both Europe and Eastern North America (*Anthracopupa*). There is a single record of a tornatellinid (*Protornatellina*) from the Cretaceous of Wyoming. Today the family has a Juan Fernandez, Eastern Polynesia, and Hawaii center of diversity, with only fringe area records elsewhere. The fact of its presence in the Paleozoic of the Northern Hemisphere is the most significant point for this study.

For both the Charopidae and Endodontidae the earliest known fossils are the Miocene taxa reported on in these studies. No fossils from other parts of the world are assignable to these groups. It is highly significant, however, that one of the North American Paleozoic land snails, *Protodiscus priscus* (Carpenter, 1867) (see Solem & Yochelson, 1979), belongs to the Discidae, a family that is derivable from the endodontid-charopid stock in terms of basic anatomy (Solem, in preparation A) but is too specialized to serve as an ancestor to the Pacific taxa. The Discidae still have a Holarctic distribution. For none of the other families of land snails found on the Pacific Islands is there fossil data that bears on their direction and time of colonization.

For two of the families endemic to the Pacific Ocean, there is thus either direct (Achatinellidae) or indirect (Endodontidae) evidence of Paleozoic origin. For two other families endemic to the Pacific, the Partulidae and Amastridae, there are no fossil records, but in anatomical structure they rank among the most generalized land snail taxa. The land snails are thus unique in terms of the Polynesian biota in having antique endemic families, rather than being basically attenuations of Oriental elements.

The pattern of land snail biogeography through time (Solem, 1979b) is one of great conservatism. For example, the Ammonitellidae and Oreohelicidae have a small Western North American distribution that has remained stable since the Cretaceous. In the same area, the urocoptid subfamily Holospirinae has shifted its distribution south by only a few hundred miles since the Cretaceous. Western Europe has shown significant deletion of snail groups since the Miocene, but this apparently is an exception to the general pattern of great stability through at least the Tertiary.

Given the above data on time and place of appearance in the fossil record, plus a general pattern of distributional stability, interpretation of the Pacific Basin land snail fauna as an old, relict situation becomes far easier to accept. Extant Pacific endodontid genera were present in the Miocene, and the families themselves are Paleozoic in relationships.

For the Achatinellidae (Pilsbry, 1900a) which have a significant Paleozoic fossil record in the Northern Hemisphere, it is not possible to hypothesize any



direction of derivation into the Pacific. The time span between the European-Eastern North American Carboniferous occurrence and their modern distribution centered on Hawaii, eastern Polynesia, and Juan Fernandez is simply too vast a span to speculate profitably on intervening events. This story is hidden by the mists of time.

For the endodontoid lineages more evidence is available. The presence of a *descendant* group in the Paleozoic of Eastern North America strongly suggests great age. The absence of endodontoid fossils from the Mesozoic and Tertiary elsewhere in the world reflects in large part the general paucity of fossil records for land snails, the general tendencies of the endodontoid taxa to occur only in moist litter conditions where the chances for successful preservation are minimal, and the basic absence of land snail fossils from the areas where endodontoids are abundant today.

With regard to the Endodontidae, there are two Pacific distribution patterns. First, the smallest and most generalized taxa (*Minidonta* and *Cookeconcha*) were present in the Marshall Islands during the Miocene and today have relatively wide distributions that, in the context of the family, are through eastern Polynesia and Hawaii. In local areas, each of which presumably were colonized by one of these minute, generalized taxa, repetitive local evolution into larger and more specialized genera and species has occurred. It is only rarely, in such taxa as the Marquesan *Taipidon* and its specialized offshoot *Planudonta* plus the Rapan radiation, that any significant anatomical specialization occurred. Given an age of more than 20 m.y. for chains such as Hawaii and the Australs, the persistence of generalized anatomical structures on these islands is extraordinary. The comparatively young Marquesas (see table LXX) do have genera that show a minor advance in structure.

The second pattern of distribution is shown by the structurally much more complex genera related to *Thaumatodon*, including *Priceconcha*, *Zyzyxdonta*, and *Aaadonta*. Their disjunctive distribution, including Palau, Lau Archipelago, and the scattered distribution of *Thaumatodon* (Solem, 1976b, p. 447, fig. 190), which has been interpreted as a "classical radiating pattern" (Solem, 1976b, p. 446), suggests a separate pattern of colonization. The exact point of origin for this colonization wave cannot be pinpointed at this time. Analysis of the Western Australian endodontoid taxa, as mentioned above (p. 61), must be completed before definitive statements can be made on whether Western Australia contains taxa transitional between the Endodontidae and Charopidae. Even if this should prove to be correct, then a colonization subsequent to the northward drift of Australia would be conceivable in either direction. Mitigating against this is the fact that Australia has a notoriously diversified and ancient ant fauna. Ants are not compatible with the existence of endodontids. A more probable explanation would be for *in situ* evolution of these more advanced endodontid

genera on the western fringes of Polynesia and Micronesia. The Tertiary subsidence over most of the Central Pacific Basin then would have conceivably resulted in the isolation of the more generalized endodontids in Eastern Polynesia and Hawaii, and more specialized taxa near the western fringes. The minor secondary waves of dispersal postulated for *Thaumatodon* (Solem, 1976b, pp. 446-448) represent a minor adjustment in range.

For the Punctidae, the few Pacific Island records are quite amenable to having resulted from accidental transport on the feet or feathers of migrating water fowl. Together with the minor Holarctic zonitoid elements in Hawaii and Tahiti reported by Baker (1941, pp. 349-352) and the succineids, these are taxa living in bog areas and/or with extra heavy and sticky mucus. Vitrinids and succineids have been found on birds, and these few taxa probably are recent migrants to the Pacific.

The Charopidae represent a more complex and varied situation. The one truly wide-ranging genus, *Discocharopa*, which extends from the Philippines to the Society Islands, is almost exactly paralleled in distribution by *Stenopylis*, a helicodiscid land snail whose other relatives are restricted to Eastern North America and the West Indies. The latter ranges from the Philippines to Solomon Islands. Both probably represent comparatively recent additions to the Pacific Basin fauna. It would not be surprising if relatives were discovered in wetter parts of China. The Rotadiscinae are represented in the Pacific by *Microcharopa* in Fiji. Elsewhere they have a Western Australian and southwestern United States to South American distribution. At present, it probably is preferable to hypothesize a Southern Hemisphere radiation, although it is almost as plausible to consider this group a relict of a worldwide fauna.

The genus *Graeffedon*, found in Samoa and Tonga, has its only known relative on St. Helena Island in the Atlantic. Additional studies are needed to determine whether some South African, Australian, and/or New Zealand taxa are closely related. This genus probably represents a classic Gondwanaland distribution.

The remainder of the Charopinae, *Sinployea* and its allies, do have close relatives in such diverse areas as New Zealand, Juan Fernandez, and South America. They represent a comparatively recent colonization of the Pacific from the New Guinea-Australian region. It is not possible at this time to assign a time or direction of arrival for the Trukcharopinae and Semperdoninae, subfamilies endemic to Micronesia, until the New Zealand-Australian radiation is better understood.

In the absence of detailed generic and subfamilial level revisions of the Australian and New Zealand charopid taxa, it is not possible to treat the charopid radiation on the Pacific Islands in a comprehensive biogeographic sense. Questions concerning their direction and time of derivation will depend upon greater phyletic knowledge than we have at this time.

On the basis of radiation patterns on the Pacific Islands, we can make a few general statements. First, successful overseas colonization by an endodontid must be an extremely rare event. For almost all of the islands, even those with the largest generic and species-level radiations and greatest ages, only single colonizations would be required to produce the known diversity. To a lesser extent, the same applies for the islands lying on the fringes of the charopid distribution, but the wider distribution of the semiarboreal *Sinployea* suggests more frequent dispersal. In both situations, because of secondary local evolution, the taxa on the fringes of distribution are larger in adult size than those found nearer the presumed core areas. It is only when such islands as Ellice, Lau, and Tonga are considered that multiple successful colonizations are required to derive the extant diversity.

Although the endodontid fauna in particular probably is of ancient persistence in the Pacific, events of the late Tertiary apparently have had a profound effect on the endodontoid fauna. As organisms from Southeast Asia have successfully colonized the islands between New Guinea and Fiji, successful survival by charopids has been restricted to extremely small-sized taxa, and apparently the endodontid fauna, if present at all in this area, became extinct.

Though it is frustrating not to be able to delineate clear directional or time changes in distribution for the endodontoids, their unusual patterns of diversification, achievement of generic diversification by the Miocene for several extant groups, and patterns of size and structure indicate a great stability for this interesting group. It is hoped that eventual revisions of the Australian and New Zealand taxa will enable development of an overall biogeographic scheme for this complex of families.

At present, to view them and the achatinellids as of Paleozoic origin in time, and probably at least Mesozoic arrival in the Pacific for the Endodontidae, is a conservative view. At least some of the Charopidae would be Tertiary immigrants.

#### PATTERNS OF SPECIES DIVERSITY

Since Preston (1962) pointed out a relationship between topographic area and the number of species present, considerable effort has been devoted to analyzing the bases of this relationship. MacArthur & Wilson (1963) introduced the concept of an island's fauna being a balance in dynamic equilibrium between colonization and extinction. This was developed further in the now-classic *The Theory of Island Biogeography* (MacArthur & Wilson, 1967). These ideas proved to be powerful tools in analyzing many questions. Among the furthest reaches were the attempts of Schopf (1974) and Simberloff (1974) to tie the massive Permian-Triassic extinctions of marine invertebrates to a marked decrease in total shallow water marine areas at that time. More recently Diamond (1977) hypoth-

esized that of all islands in the Pacific area, only New Guinea, Madagascar, and possibly New Zealand were large enough for speciation on the same island to occur in birds. In all other instances he concluded that speciation in Pacific birds seems to have taken place on separate islands or in separate archipelagoes, with congeneric sympatry the result of multiple colonizations.

Comparatively little has been published relating these ideas to mollusks. Peake (1969, figs. 19, 25-26) graphed the species-area relationship for land snails from selected islands of Indonesia and Melanesia, using available data from scattered faunistic reports. Subsequently, Peake (1971) performed the same type of analysis for birds, terrestrial mollusks, and certain insects from islands of the Western Indian Ocean. Solem (1973e) gave a preliminary summary of the fact that Polynesian land snails do not follow the species-area curve. Lassen (1975) analyzed the freshwater snail fauna in Danish ponds. Otherwise, there is no relevant malacological literature.

Almost all reports on species area and equilibria have stopped short of analyzing adequately the basic hypotheses underlying the phenomenon. At the time of writing this review (1978), Connor & Simberloff (1978) had just published a detailed analysis on the Galapagos flora and avifauna, pointing out problems in relation to the adequacy of sampling and species lists. But this deals with only part of the problem. Most literature has been concerned with organisms that have been sampled without regard to what may be best termed the "Crusoe effect." Although Robinson Crusoe was an effective resident on Juan Fernandez for a period of years, he was far from being a successful colonizer in the sense of establishing a permanent reproducing population. The collecting of an individual organism during a biotic survey tells nothing about its status in terms of a viable population. From the standpoint of sampling surveys, it is extremely difficult to distinguish immediately between chance strandeers ("Crusoes"), life-time residents but not reproducers, and actual colonizers (breeding populations established). Thus, some of the reports on which calculation of turnover rates have been calculated, such as the classic studies of Simberloff & Wilson (1969), Simberloff (1970, 1976a, b, 1978), and Diamond & May (1977) may in large part have a data base consisting of "Crusoes" rather than inhabitants.

Another factor affecting the species diversity on an island area is one on which I have been unable to locate adequate statistical data. Common sense says that the minimum area needed to support a permanent population of field mice, such that the species could be expected to survive the random fluctuations in population numbers that are an inevitable part of living in an unstable environment, is considerably smaller than the area needed to maintain an equivalent permanent breeding population of tigers. Whereas the former might be as low as a few acres or even less, the latter



might require many thousands of square miles. Since much of the observational work on the species-area relationship has been dealing with very small islands and comparatively large vertebrates, the effect of the above phenomenon has yet to be adequately accounted for in predictions and discussions.

Another problem was initially pointed out by Wilson & Taylor (1967a) but seems to have been completely ignored by subsequent workers. In their analysis of species-area diversity in the Polynesian ant fauna, they noted that inclusion of the endemic ants from Samoa greatly skewed the species-area curve produced by a consideration solely of the introduced ants. The effect of local speciation upon diversity levels in relation to area has not, to my knowledge, been considered subsequently.

The species-area curve and equilibrium biogeographical theory are highly useful and predictive models when dealing with a limited set of circumstances. These may be defined as: In the absence of local speciation, when the area available is close to or below the minimum area needed for long-term maintenance of a viable species population, and when at least part of the species are represented by "Crusoes" rather than colonizers.

The land snails of the Pacific Islands represent a contrasting situation in which: Colonization rates are apparently very low, local speciation and even generic diversification has been extensive, and practically none of the areas are at or below the minimum area needed to maintain a long-term population. Examination of this quite different situation is thus of general interest.

Although only marginally considered in the following analysis, brief notice must be made of some patterns shown by land snails brought to Pacific Islands by Caucasian commerce within the past one and a half centuries. As early as the 1830s, African and West Indian subulinids were introduced onto Pacific Islands. Within a few decades these species had penetrated even the densest native forests and reached the mountain tops. By the 1890s, other species from Indonesia and/or Africa started a second round of introductions. Between the 1920s and the 1960s, some of the original introductions became restricted to mountain peaks (Upolu) or actually became totally replaced (Tutuila) by the later colonizers (Solem, unpublished data). The facts of rapid change among introduced taxa have bearing on this discussion for two reasons. First, they demonstrate that many of the families not "naturally" represented on the Pacific Islands—Subulinidae, Streptaxidae, Achatinidae, Oleacinidae, Arionidae, Limacidae, Bradybaenidae, and Helicidae—can, once introduced, thrive on Pacific Islands. They never reached the islands until human beings intervened. Second, they demonstrate once again the unstable nature of disparate faunal elements introduced onto islands. This has been pointed out by numerous investigators in the past decade.

As in most studies on species diversity, the data base for Pacific Island land snails is imperfect. For most of the Pacific Islands, publication of faunal lists is very incomplete. This is partly the result of extinction prior to adequate sampling (see discussion on Rapa, p. 282), partly because collected materials have not yet been published (on Mangareva, Micronesia, and Fiji Expeditions from the Bishop Museum in the 1930s), and partly because collecting efforts still are inadequate. It has thus been necessary to utilize two different sets of data in the following analysis. First, there are islands for which reasonably adequate faunistic reports exist or materials available in the Bishop Museum and Field Museum of Natural History permitted reasonable assessment of total land snail diversity levels. Data on these islands are presented in Figure 140. Second, there are families of land snails in the Pacific for which reasonably comprehensive published distributional data exist. For these families, it was possible to tabulate the diversity for a much greater number of islands (figures 141–143). The families for which comprehensive data were available are listed in Table LXXI. None of these families have an ancestor-descendant relationship on the Pacific Islands, and thus they have basically independent biogeographic histories. All of the systematic revisions used the collection resources of the B. P. Bishop Museum; several were supplemented by Field Museum of Natural History collecting efforts in the 1960s and 1970s. The sources for the basic data on the revised families are: Tornatellinidae (Cooke & Kondo, 1960, Kondo, 1962); Partulidae (Kondo, 1968); Endodontidae (Solem, 1976b, 1977a, in preparation C); Punctidae (this report); Charopidae (this report); Helicarionidae and Zonitidae (H. B. Baker, 1938, 1940, 1941). Baker's report makes only minor use of the Henry G. Lapham Expedition material collected on Fiji and Lau in the late 1930s and thus is not completely comparable to the other studies. The net effect of this omission probably is minor. Its correction would have slightly increased the diversity levels reported from Fiji and Lau. I do not consider this a major defect in the

TABLE LXXI. — PACIFIC ISLAND LAND SNAIL FAMILIES WITH COMPREHENSIVE DISTRIBUTIONAL DATA AVAILABLE

Order Orthurethra
Family Tornatellinidae
Family Partulidae
Order Sigmurethra
Superfamily Arionacea
Family Endodontidae
Family Punctidae
Family Charopidae
Superfamily Limacacea
Family Helicarionidae
(& Euconulidae and Microcystidae)
Family Zonitidae
(& Trochomorphidae)

analysis. These data are used for Figures 141–143 and in Tables LXXIV–LXXVI.

The data set on total land snail diversity comes from a huge variety of sources. Where published monographic data exists, updated figures were taken from the references listed in the preceding paragraphs. Diversity levels in Samoa and Fiji were determined from assessing 1960s and 1970s collecting efforts, plus the classic faunistic accounts by Garrett (1881, 1884, 1887a, b). Additional data were taken from the work of Germain (1932, 1934) and Gude (1913) for Fiji. Data on the Cook and Society Islands was obtained mainly from the works of Garrett (1881, 1884) and the systematic reviews listed above. For the key islands of Rapa and Lord Howe, diversity estimates were based, respectively, on both published and unpublished records in the B. P. Bishop Museum and collections made for Field Museum of Natural History in 1963 by L. Price, because the only faunistic report in this century (Iredale, 1944) vastly oversplit the species and genera. Subsequent collecting on Lord Howe by staff of the Australian Museum, Sydney, has produced many additional species (personal communications). My estimate of total land snail diversity on Lord Howe is far too conservative, but the necessary systematic revisions have not been made. Correction of the cited figures has not been attempted to reflect the greater diversity.

As indicated above in the faunistic reviews (pp. 275–301), the adequacy of collecting efforts for most large islands is suspect, so that the levels of speciation reported here are underestimates, not overestimates. This point cannot be overemphasized. The main inadequacy of the data base is that the following discussion is based on a conservative view of actual diversity levels, and the true figures would be significantly higher.

In its classic expression, the species/area equation is:  $S = CA^z$ , where  $S$  = the number of species;  $C$  = a variable constant, usually under 10;  $A$  = the island area;  $z$  = a constant ranging from 0.10–0.489, normally about 0.27. As indicator islands for high diversity level, it is instructive to consider the fauna of Oahu (table LXVII), representing a large island with high diversity, Rapa (table LXIX), which is a relatively small island with very high diversity, Lord Howe Island (table LXXII) as a very small island with high diversity, plus Upolu and Viti Levu (table LXXII) as large to extremely large islands with low diversity. Table LXXIII is an attempt to fiddle with the basic formula and thus match observed, as opposed to calculated, diversity levels. Two exercises have been attempted: First using the most common form of the equation, then attempting to predict the observed diversity of Lord Howe and Rapa by modifying the two variable constants. It is evident that the land snail diversity on these three islands does not follow the predicted formula and does not match a gross alteration of the variable constants. The reasons for this will be dealt with subsequently.

TABLE LXXII. – LAND SNAIL FAUNAS OF LORD HOWE, UPOLU AND VITI LEVU

Taxon	Island		
	Lord Howe	Upolu	Viti Levu
Prosobranchs	11	13	23
Tornatellinidae	3	2	1
Pupillidae	–	2	2
Partulidae	–	5	–
Endodontidae	–	1	–
Punctidae	ca. 5	–	–
Charopidae	ca. 15	4	7
Helicarionidae and Zonitidae	14	10	15
Succineidae	–	3	–
Bulimulidae	1	–	6
Introduced	2	4	4
TOTALS	51	44	58
Area in square miles	5	430	4,011

TABLE LXXIII. – CALCULATED AND OBSERVED MAXIMUM DENSITY OF LAND SNAIL SPECIES

	Calculated		Observed	Area in square miles
	$S = 10A^{0.27}$	$S = 18.6A^{0.63}$		
Lord Howe	15	51	51	5
Rapa	21	99	100	14.2
Oahu	56	1,045	395	605

Figures 140 and 141 present species diversity plotted against area in a double log plot. Figure 140 covers those islands for which estimates of the total fauna of land snails could be attained. The diagonal line represents a calculated level of diversity using the basic

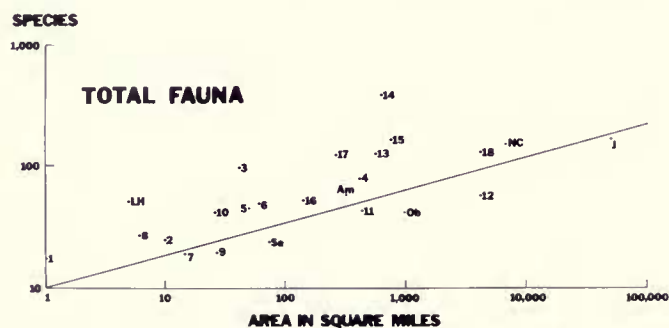


FIG. 140. Species-area relationships for total land snail faunas of selected Pacific Islands. Data from many sources. Straight line plots the classic formulation  $S = 10A^{0.27}$ . Note the large faunas on Lord Howe (LH), Rapa (3), and most Hawaiian Islands (13–17). Island codes for Polynesia are: (1) Henderson; (2) Makatea; (3) Rapa; (4) Tahiti; (5) Moorea; (6) Raiatea; (7) Atiu; (8) Aitutaki; (9) Mangaia; (10) Rarotonga; (11) Upolu; (12) Viti Levu; (13) Kauai; (14) Oahu; (15) Maui; (16) Lanai; (17) Molokai; and (18) Hawaii. Extralimital islands for comparison are: (AM) Ambon; (J) Java; (LH) Lord Howe; (NC) New Caledonia; (OB) Obi; and (SA) Saparua.



species/area equation. The tendency for nearly all islands to lie above the predicted diversity level is obvious. The extent of diversity on Lord Howe (LH), Rapa (3), and most of the Hawaiian Islands (13–17) is obvious. Although there is a slight increment in species number with increased area, this plot greatly oversimplifies an actual situation.

Figure 141 gives the same type of plot for species from the recently monographed families listed in Table LXXI. Here there is even less of a clear-cut pattern for increase in diversity to accompany increase in island size. Subsequent to the preparation of these figures, the material from small islands of the Lau Archipelago reported on by Solem (1978a) was obtained and studied. Lakemba, with 22 square miles, had 20 species, whereas Karoni, with approximately 0.25 square miles, had 19 species collected. Addition of these records to Figure 140 would have even more clearly demonstrated the lack of "concordance."

Further manipulation of the data is presented in Figures 142–143 and Tables LXXIV–LXXVI. By grouping the islands plotted in Figure 141 into area classes, it is possible to plot the number of species recorded in relation to average island size. The clusters are those into which the islands grouped naturally, rather than following any arithmetic progression. With relation only to area, it is evident that an island of less than 4.5 square miles has low diversity, there is

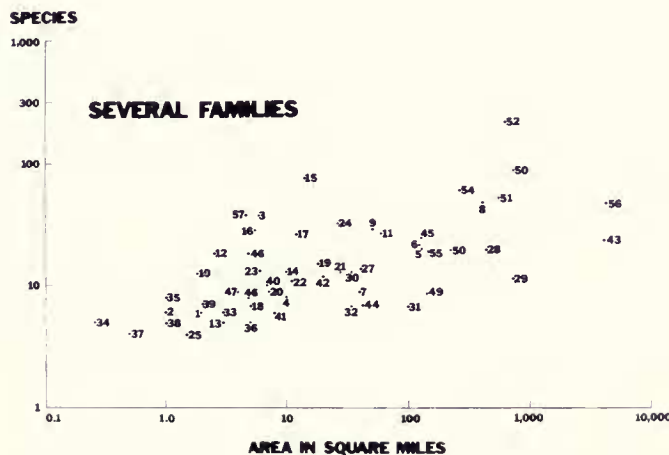


FIG. 141. Species-area relationships for selected land snail families on Polynesian and Micronesian islands. Data from families listed in Table LXXI. Island codes are: OUTER POLYNESIA, (1) Pitcairn, (2) Henderson, (3) Mangareva, (4) Makatea; MARQUESAS, (5) Nukuhiva, (6) Hivaoa, (7) Uapou; SOCIETY ISLANDS, (8) Tahiti, (9) Moorea, (10) Tahaa, (11) Raiatea, (12) Huahine, (13) Maupiti, (14) Borabora; AUSTRAL ISLANDS, (15) Rapa, (16) Rututu, (17) Raivavae, (18) Rimatara, (19) Tubuai; COOK ISLANDS, (20) Mauke, (21) Mangaia, (22) Atiu, (23) Aitutaki, (24) Rarotonga; SAMOA, (25) Olosega, (26) Ta'u, (27) Tutuila, (28) Upolu, (29) Savai'i; TONGA, (30) Eua, (31) Tongatapu, (32) Vava'u; LAU ARCHIPELAGO, (33) Wangava, (34) Navutu-i-Loma, (35) Yangasa Levu, (36) Namuka, (37) Karoni, (38) Aiwa, (39) Oneata, (40) Nayau, (41) Mango, (42) Vanua Mbalavu; FIJI, (43) Viti Levu; CAROLINE ISLANDS, (44) Kusaie, (45) Ponape; PALAU GROUP, (46) Peleliu, (47) Angaur, (48) Koror, (49) Babelthuap; MARIANAS, (50) Guam; HAWAIIAN ISLANDS, (51) Kauai, (52) Oahu, (53) Maui, (54) Molokai, (55) Lanai, (56) Hawaii. For comparison, (57) Lord Howe Island off Australia.

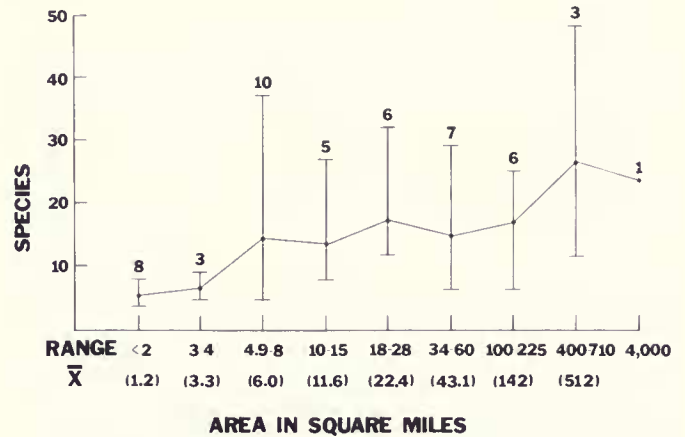


FIG. 142. Species diversity in islands grouped by size, using data from recently monographed families listed in Table LXXI. Number above each bar indicates the number of islands in that size class, the bar indicates the range in species numbers. Hawaiian Islands, Lord Howe Island, and Rapa omitted because of the distortion produced by their high diversity.

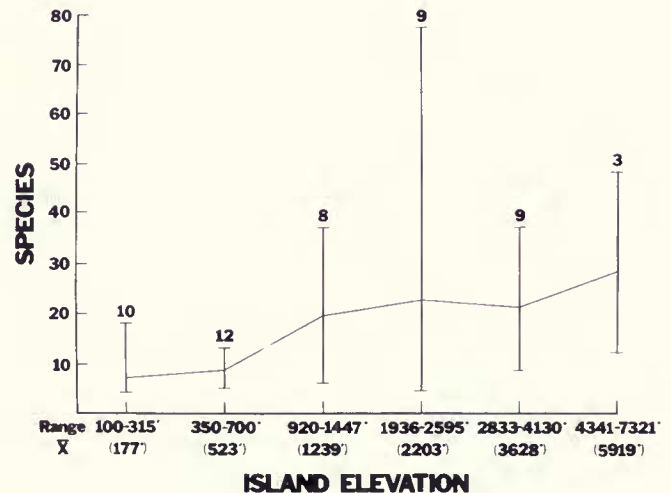


FIG. 143. Species diversity in islands grouped by elevation, using data from recently monographed families listed in Table LXXI. Number above each bar indicates the number of islands in that elevation range. Lord Howe and Hawaiian Islands omitted because of the distortion produced by their high diversity.

a significant jump in diversity when an island reaches 4.9 miles in area, but essentially no additional change in diversity levels until an island size of 400 square miles is reached. Figure 143 gives the same type of plot relating species diversity to island elevation. Again, the intervals of the clusters were determined by self-grouping of the data. The results are simple: low diversity under 700 ft. elevation, moderately high diversity over 900 ft. elevation. A simple refinement of the data is presented in Table LXXIV where island area is compared with islands of under 1,000 ft. elevation and over 1,300 ft. elevation. Regardless of island size, there is relatively low diversity under 1,000 ft. elevation. The bulge in the 18–28 square mile category is caused by a series of relatively low islands clustered near larger and higher ones. For islands of over 1,300 ft. elevation, diversity of land snails decreases once an island size of

TABLE LXXIV. - CORRELATION BETWEEN ISLAND SIZE, ELEVATION, AND NUMBER OF LAND SNAIL SPECIES

Island area in miles <sup>2</sup>	Mean Number of Species when Elevation is:	
	Under 1,000 feet	Over 1,300 feet
4.9-8	9.5	34.3
10-15	9.5	31.5
18-28	12.5	20.0
34-60	7.0	16.5
100-225	8.0	21.8

more than 15 square miles is reached, which is exactly contrary to what conventional wisdom would predict.

Another aspect of the conventional wisdom is that islands nearer the hypothesized center from which colonization occurs should have higher diversity than islands of equal size that are further away. Data regarding the total land snail fauna for two pairs of similar-sized islands are given in Table LXXV. As pointed out by Solem (1959b), most of the land snail families now in the Pacific area can be traced back to Southeast Asia. The major exception concerns the endemic families so prominently mentioned above. Tahiti and Upolu differ in total area by only 28 square miles (7%). Upolu reaches only 3,608 ft. elevation; Tahiti's highest peak is 7,321 ft. I can, however, detect no pattern or change in diversity once an elevation of 1,300 ft. elevation has been attained. Upolu is significantly nearer the general area of colonization than Tahiti, yet the latter island has almost twice as many land snail species recorded from it. My collecting efforts on Upolu failed to reveal any significant instances of geographic speciation, yet a number of such changes are known on Tahiti. Hawaii and Viti Levu are virtually identical in size (less than 0.5% difference), yet Hawaii has more than twice the number of land snail species found on Viti Levu. Hawaii has an estimated age of much less than 1 m.y. (Stearns, 1978a, b), whereas Viti Levu is at least Eocene age (Menard & Hamilton, 1963, p. 201, table 1), yet the former has many more land mollusks.

Quite in contrast to what would be predicted, it is evident that isolated, small islands have the highest levels of diversity recorded (table LXXVI).

Although Peake (1971, fig. 9) pointed out that the diversity of land snails is lower on low islands in the Indian Ocean than on neighboring high islands, the above results on the reverse correlation of island area with species diversity, the triggering of high diversity at 1,000+ ft. elevation, and the greater diversity on more isolated islands or islands that are further from the basic source fauna represent very different situations from those encountered in studies dealing with other taxa.

TABLE LXXV. - LAND SNAIL DIVERSITY ON ISLANDS OF SAME SIZE BUT DIFFERENT DISTANCES FROM INDONESIAN-MELANESIAN CORE

Island	Area	Families	Total Species
Tahiti	402	12	80
Upolu	430	14	44
Hawaii	4,030	10	128
Viti Levu	4,011	15	58

The reasons for this are very simple. Land snails are highly sensitive to a lack of moisture. Because rainfall on oceanic islands increases with altitude at a far greater rate than simple linear accretion, the high rainfall on the 1,000+ ft. islands results in a far more favorable climate under which local speciation can occur. Because so few islands under 4.9 square miles have been studied, it is premature to pick that size as being the minimum at which extensive local land snail speciation can occur. The data from Lord Howe Island and Rapa do show conclusively that such small islands are more than adequate for land snail speciation to take place *in situ*. The higher diversity on more isolated islands probably relates to a simple phenomenon: The more isolated the island, the less frequent will be new colonizations. Each new colonization represents a potential for actual disturbance of the ecosystem. The effect of periodic disturbance on shallow water marine community diversity is well documented in a number of studies. At a limited level, it can maintain a high diversity, but if carried too far it can result in lower diversity. I view the isolated high islands as land snail havens whose tranquility and stability over several millions of years permitted extensive and luxuriant speciation to occur. The absence of disturbance or new colonizers permitted niche subdividing, resulting in the great degree of sympatry recorded in these studies on Mangareva and Rapa (see pp. 280, 282). The fragility of the complex and finely divided ecosystems is at-

TABLE LXXVI. - DIVERSITY OF LAND SNAILS ON SMALL ISOLATED ISLANDS

## DIVERSITY IN SELECTED FAMILIES

Island	Area in miles <sup>2</sup>	Species	Elevation in feet
Lord Howe	5	37	2,833
Rurutu	5.5	29	1,300
Mangareva	6	37	1,447
Raivavae	12	27	1,434
Rapa	14.2	77	2,097



tested to by the rapidity of their destruction in the last 200 years.

In contrast to the isolated outer islands with high diversity levels, such islands as Upolu and Viti Levu have been subject to repetitive disturbances from new colonizers. I suspect that this accounts for the lack of local speciation among most of their land snail taxa.

The species-area differences shown by the land snails on Pacific Islands are the result of extensive speciation from rare colonizers evolving in isolation. Their tragedy was non-adaptiveness to changing conditions.

#### SUMMARY OF ZOOGEOGRAPHY

The endodontoid land snails of the Pacific Islands present an extremely high level of both generic and specific endemism, with only one species of 290 reviewed and only five (*Lagivala*, *Sinployea*, *Discocharopa*, *Palline*, and *Punctum*) of the 46 genera recognized for Pacific Endodontidae, Charopidae, and Punctidae occurring extralimitally. This diversity resulted from extensive local speciation, particularly in the more isolated islands and those furthest from the Indonesian-Melanesian core region. Frequently the entire fauna on an island group could have evolved from a single colonizer.

The high levels of diversity on such islands as Mangareva (25 species-level taxa) and Rapa (24 species-level taxa) resulted in considerable sympatry, with, respectively, maximums of 12 and seven species taken from a single highly restricted station. The nature of niche partitioning is unknown and cannot be studied because of extinctions. Accompanying the high specific and generic diversity in both the Endodontidae

and Charopidae was a tendency for evolution of large-sized species and genera. The Endodontidae show a repetitive independent evolution of an umbilical brood chamber from the shell umbilicus.

The endemic Achatinellidae are known to be of Holarctic Paleozoic origin (Solem & Yochelson, 1979). The Endodontidae have only a Miocene direct fossil record, but they are anatomically more generalized than both the descendent Charopidae and the probably descendent Discidae, which also has a Paleozoic record (Solem & Yochelson, 1979). Because many Pacific Islands (table LXX) are known to have an age of more than 20 m.y. and the existence of land in the Pacific area predates the Tertiary, the acceptance of these as ancient relicts adapted to rare successful colonization from island to island is proposed. Because of the scarce fossil record elsewhere, absence of detailed revisions for the Australian-New Zealand taxa, and lack of recognized descendant groups, questions of direction and time of spread cannot be answered adequately at this time.

In relation to species-area and equilibrium biogeography theory, the Pacific Island land snails do not conform to theoretical predictions. They are most diverse on small isolated islands. Islands further from the Indonesian-Melanesian core area have higher diversity than those of equal size that are nearer. Elevation of more than 900 ft. is a trigger for land snail diversity, and islands of 4.9 to 15 square miles in area have the greatest diversity of land snail taxa. The above departures from theory probably resulted from extensive local speciation in the absence of competitors and predators. This seems to have occurred most extensively on the small, more isolated islands.

## SUMMARY

The 87 species-level taxa found on the islands of Micronesia and Polynesia that belong to the Punctidae and Charopidae are revised in detail. In addition, 11 taxa that either are extralimital members of a genus with endemic species in the area studied or that extend into the area from Indonesia and Melanesia, *Discocharopa aperta* (Möllerndorff, 1888), are reviewed. A total of 19 (of 21) genera and 50 (of 98) species-level taxa are described as new. Three taxa probably are new, but because of very limited material have not been named. Five named taxa from the mid-1800s could not be identified from published data or from any material located in museums, and these names are listed as *incertae sedis*.

Basic anatomical and conchological differences among the Punctidae, Charopidae, and Endodontidae are reviewed, with new definitions of the first two families presented. Differences in the frequency and structure of the apertural barriers, pattern of whorl width increment, formation of shell microsculpture, and growth patterns are discussed. The anatomical patterns in the pallial region are interpreted as indicating progressive evolution, and the structural changes in the genitalia of the Charopidae and Endodontidae are interpreted in relation to space and shell growth differences.

The Charopidae is shown to be represented in the Pacific area by at least four subfamilies, Rotadiscinae Baker, 1927, Charopinae Hutton, 1884, Trukcharo-

pinae, new subfamily, and Semperdoninae, new subfamily. Further subdivision of the Charopinae depends upon studies of the Australian and New Zealand taxa.

Fossil endodontoid land snails from Midway, Funafuti, Bikini, and Eniwetok, ranging in age from Miocene to Pleistocene, are shown to belong to extant genera and species groups, except for *Protoendodonta* Solem, 1977. They show that the Tertiary subsidence of the Central Pacific has resulted in the extinction of species and contraction of ranges for many of the genera.

The diversity of the endodontoid land snails is analyzed in terms of species numbers, generic splitting, shell size in each area, and minimum numbers of colonizations required. Higher diversity occurs on more isolated islands and islands with an elevation of over 1,000 ft. Mean adult size of species is largest on the fringes of present distribution. The greatest land snail diversity is found on islands of 5 to 15 square miles, with large islands having lowered diversity. Most of the outer islands could have achieved their current diversity from a single successful colonization.

The pattern of land snail diversity does not conform to the species-area curve or to the predictions of equilibrium biogeography because of extensive *in situ* speciation on the high islands of the Pacific. It is proposed, on the basis of the fossil record of other taxa, that the endodontids represent pre-Tertiary survivors in the Pacific Basin and that the Charopidae are Late Mesozoic to mid-Tertiary colonizers.



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## APPENDIX

Explanations of anatomical abbreviations used on illustrations.

A - anus	MG - mantle glands
B - buccal mass	MR - mantle lappet
BE - esophagus	OG - salivary glands
BR - buccal retractor muscle	OD - salivary gland ducts
CF - caudal foss	P - penis
CH - caudal horn	PC - penis pocket caecum
CR - columellar retractor muscle	PP - penial stimulator, papilla or pilaster
DE - pore from vas deferens to epiphallus	PR - penial retractor muscle
DG - prostate	PS - penis sheath
DP - vas opening into penis	PV - verge
E - epiphallus	PVS - penial verge sheath
EP - pore from epiphallus into penis	PZ - flaps inside penis by vas opening
EPP - pilasters in epiphallus	S - spermathecal shaft and its sac
F - foot	SO - pore from spermatheca
FR - foot retractor muscle	SP - sperm packet
FS - foot grooves	SPP - pilasters in spermatheca
G - ovotestis	TE - ommatophores
GD - hermaphroditic duct	TER - ommatophoral retractor muscle
GG - albumen gland and ducts	TV - rhinophoral tentacle
GT - talon	TVR - rhinophoral retractor muscle
H - heart	UT - uterus
HG - hindgut or rectum	UT <sub>1</sub> - section of uterus
HV - principal pulmonary vein	UT <sub>2</sub> - section of uterus
I - intestine	UT <sub>3</sub> - section of uterus
IZ - stomach	UT <sub>4</sub> - section of uterus
J - jaw	UV - free or postuterine oviduct
K - kidney	UVO - pore of free oviduct
KD - ureter	V - vagina
KX - ureteric pore	VC - vaginal caecum
LK - urinary sinus	VD - vas deferens
LM - diaphragm	VRM - vaginal retractor muscle
LP - pneumostome	VS - vaginal stimulator
M - mantle edge	X - carrefour
MA - mantle lappet	Y - genital atrium
MC - mantle collar	Z - digestive gland or liver
MD - mantle retractor muscle	



# INDICES

Two indices are presented, a geographic and a systematic. The geographic lists every reference to that unit in the monograph, whether in text, table, or figure legend. The principal geographic discussion of a fauna is indicated by boldface type for a convenient guide to

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